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THE INHERITANCE OF THYROID SIZE AND THE ESTABLISHMENT OF THYROID RACES IN RING DOVES

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THYROID size is so readily influenced by so many adventitious factors—such as altitude, diet, season, state of nutrition, insanitary surroundings, iodine intake, age, intestinal flora, activity of other endocrine organs, disease and by sexual and even by psychic states—that the rôle of genetic factors in determining thyroid size is a most difficult thing to investigate. Moreover, a large thyroid may belong to either of two sharply opposed states of thyroid function, and the genetic factor or factors in hypo- and hyper-functioning glands are not necessarily the same factors. Thus, a genetic analysis of thyroid size presupposes the elimination—or the vigorous leveling—of many physiological factors, and the sharp differentiation of at least two types of thyroid enlargement and function.

Inheritance studies on this organ have hitherto been concerned almost solely with simple (endemic) goiter, and with this disorder as it is exhibited in man, though it is well known that goiter occurs in various animals. In most of these studies the presence of affected individuals in several successive generations of certain families is reported; this, together with the finding of a much smaller incidence of goiter in the general local population, is utilized to provide a probability of actual inheri-

tance (Riebold, 1915; von Siemens, 1917; Bluhm, 1921; Lloyd, 1924; Brain, 1927). These and other workers have remarked on some of the inherent difficulties of such data; but the workers mentioned quite properly urge that a hereditary influence is probably involved. In some of these early studies it was even thought possible to conclude that simple goiter in man is a recessive sex-linked character. More definite tests of the existence of a genetic influence in goiter have been recently supplied by von Siemens (1924; 1925) and Weitz (1924) through their studies on the thyroids of uniovular twins. In such twins the thyroids are almost always of similar size and appearance, while the thyroids of binovular twins are frequently different. These two studies may be said to mark the high point in our present information concerning the genetics of simple goiter, since they demonstrate, beyond question, that a genetic factor (or factors) is one of the many factors concerned in the production of simple goiter. The heredity of hyperthyroidism (exophthalmic goiter) has apparently not been studied.

The establishment of "thyroid races" in an organism has not hitherto been accomplished and demonstrated. The present study, including preliminary reports (Riddle, 1926, 1927) upon some of the races fully described in this paper, appears to be the only attempt thus far made to establish any race on the basis of the size of an endocrine organ. Possibly bearing on this point is the fact that the normal thyroids of the Japanese are known to be much smaller than those of Europeans, but it is entirely unknown whether this difference is based upon a genetic or upon one or many of the above-mentioned physiological factors. Our success in establishing thyroid races, even as this was shown in our preliminary reports, has of course supplied excellent evidence that genetic factors are involved in the determination of thyroid size. The results fully presented here not only provide the necessary data concerning the formation of large or small

"thyroid races," but they further show for the first time the behavior of thyroid size in crosses.

Considered in a more general way this communication is a partial account of an attempt begun several years ago to establish races of large and small size of thyroid and of pituitary among strains of both ring doves and common pigeons. Twenty-four different pairs of ring doves and thirteen pairs of common pigeons were taken as the foundation for an equal number of such endocrine races or strains. This account can not consider the results obtained on pituitary size in either doves or pigeons, nor of thyroid size in the common pigeons. Only what has been accomplished with thyroid size and its behavior in crosses in twenty-four ring dove races is attempted here. If, however, it is realized that the entire study has involved thirty-seven races, and an even greater number of kinds of hybrids—requiring therefore the simultaneous breeding of these numerous classes—it will become evident that large numbers of offspring may not be expected for any one generation of any one race or kind of hybrid. In the aggregate, however, the thyroids of nearly two thousand *healthy* doves have been weighed and utilized in this study.

Initial Considerations

Unless the well-known causes of temporary and permanent change in thyroid size have been continuously and faithfully eliminated or leveled in our studies it is not possible to consider our measurements as having any proved or particular value as a study of the inheritance factor. A brief description of the conditions under which our birds lived, and of the precautions taken to secure valid data, must therefore be supplied at once.

Diet.—Doves and pigeons are by nature peculiarly well adapted to thyroid studies because of the fact that they will feed upon precisely *the same dry grains during every day of the year,* and this diet can be and has been kept quite the same from year to year. If the dietary

habits of these birds had been otherwise it is doubtful whether the present study would have been undertaken. The water supply was from a driven well. Water from the same source was used at all seasons and throughout the several years involved in this study.

Cleanliness.—The cages in which these birds were reared, and those in which they lived after maturity, have been kept clean—and essentially dry. The floor of every cage is kept continuously covered with a deep layer of clean dry sand. This sand, which quickly absorbs and dries the excreta of the birds, is frequently removed and replaced with a fresh supply. The water which the birds drink, and in which they bathe, is so guarded as to permit the wetting of but a small fraction of the floor-space of the ample cages used.

Season.—From the outset it was realized that thyroid size probably varies in one and the same bird according to season. Birds of each race therefore should be killed in fairly equal numbers at all seasons, and this method has been followed throughout the study. Later, Riddle and Fisher (1925) definitely demonstrated that the thyroids of both doves and pigeons undergo a considerable enlargement in winter and a reduction of weight in summer.

Age.—Excepting the birds used as the foundation of the various races or strains, our animals were killed for examination before they attained advanced age. These birds may live to one hundred months or more. For the purposes of our general study—of both thyroids and pituitaries—we have sought to use mature birds aged less than thirty months. These birds may rarely become mature as early as four months. More than 95 per cent. of the birds utilized in this study were more than six and less than thirty months old. We have thus greatly restricted the size variations of individual thyroids due to the age factor. Riddle and Fisher (1925) showed that thyroids of doves and pigeons aged thirty to ninety months are in general notably larger than those of

younger birds. We shall presently see that, on the average, some *races* have been killed for measurement at an earlier age than have other races; that matter will be discussed later.

Captivity or confinement.—I am aware of no study of the effects of various degrees of confinement or caging of an animal on its thyroid size. Some unpublished observations on doves, however, suggest that confinement for even a few weeks in very small space is accompanied by marked changes in thyroid size. It is, therefore, necessary to note that the present data were obtained from birds given ample space for flight, in cages essentially uniform in size, and that none of the racial or hybrid differences described here is traceable either to very close or to a variable degree of confinement.

Miscellaneous factors.—All these races have been bred continuously at the same spot—four or five meters above sea-level—so that differences in altitude and climate are excluded as agents responsible for their divergence in thyroid size. Our system of keeping many young birds together in a large common pen until mature, and then placing a single male and female together in a breeding pen (where they are left till the time their thyroids are examined), would seem sufficient to equalize most sexual and psychical states to which the various races and hybrids were subjected. We have almost completely avoided the utilization of birds in two important stages of the reproductive cycle—namely, during incubating and while feeding young.

Disease.—In birds dead of disease the size of the thyroid can not be considered normal. We have obtained thyroid weights from some dead birds, but all these are rejected for the purposes of this study. It is of even greater importance that careful autopsies (macroscopic, obtaining weights of several organs) be made, and that all birds found frankly diseased at such internal examination be similarly rejected. This has been done throughout this study. When the exact age is known

(and this is indispensable), the condition and weight of the body, gonads, thymus, liver, spleen and intestine supply an adequately trained observer with excellent criteria for the exclusion of the abnormal and diseased. The presence of considerable numbers of round worms (*Ascaridia*), or of tuberculous or other tumors, easily and automatically excludes the bird from the group of normals. We have found that the thyroids of diseased doves are usually larger, and certainly much more variable in size, than the thyroids of healthy doves. Specifically, while obtaining the thyroid weights of the 1,317 healthy birds belonging to the twenty-four races of Table I we also obtained such weights from 273 diseased birds distributed among these races. The mean racial size of the thyroids of the diseased birds is 17 per cent. larger than that of the healthy birds; the mean body weight of these same diseased doves is 16 per cent. below that of the normals.

The Original Stock and the Special Probabilities that It Included a Basis for Various Endocrine Races

At the outset of this investigation we had a rich variety of material with which to undertake a study of this kind. The ancestry of all this material was known. In addition, during ten preceding years we had obtained—because of its bearing on the sex studies then in progress—the full reproductive history of all the ring doves of our colony. During the two immediately preceding years (1919–21) much attention had been given to the several different types of reproductive disorder or abnormality that had developed in this colony of birds during many years of close observation. As a result of these studies it was concluded that the various types of disordered reproduction were ascribable neither to nutritional deficiency nor to infection. Thus by exclusion our attention was directed to their probable origin in endocrine disorder. We were very soon able to trace the origin of one rare type of such

abnormality to the thymus (Riddle, 1924), and in the intervening years our laboratory has been able to show that nearly all the organs of internal secretion are intimately connected with the processes of reproduction (Riddle, 1927b, 1929).

Besides the supply of individuals (females particularly) which had shown one or another type of abnormal reproduction, there was at hand a still larger supply of individuals whose reproduction was known to be quite normal. Both types of individuals were utilized as starting-points for one or another of the twenty-four races which are of special concern in this study. A consideration of the reproductive normality or abnormality of each of the pairs used for the foundation of these twenty-four races would consume much space, and since this description must later be given in connection with an account of the basal metabolism of these races—as this is now being determined—this will not be discussed here.

It appears that a description of the exact ancestry and relationship of the two birds used as the starting-point for these twenty-four races would unduly lengthen this publication, and only a somewhat condensed account will be attempted. The two members of the various pairs were of many degrees of consanguinity; in a few cases the members of the pair were wholly unrelated, except in the sense that they were of the same species. Races 11, 163, 44, 69, N2 and 1 originated in brother-to-sister matings. Races 6 and 29 were from matings of mother and son, while races 51 and 61 began with matings of father and daughter. A single female, mated to two different males, was the starting-point of races 63 and 63a; the same is true for races O and OT. Races 163 and 61 were derived from the same male mated to two different females. The ten additional races each started with the two birds which had happened to be the parents of an interesting progeny or a distinctive reproductive record. In our descriptions of breeding data the pairs thus

selected as starting-points are considered as P_1 and their offspring as F_1 of the strain or race.

Other significant items concerning interracial relationships in this material may be indicated. The father and mother of race 63a are related (five eighths common ancestry) and both these birds carry nearly three fourths the same blood as that of the two parents of race N2. Nearly three fourths of the ancestry of race NE is also shared by races 63a and N2. Thus these three races are closely related, and their descendants have been found to have thyroids of very nearly equal size. Races O and OT have three parts in four of common blood; the same is true of races 11 and 63, and of races 72 and 67. Races 29 and 36 carry five in eight parts of common blood. The four parents of races 44 and 1 were all brothers and sisters. All the above-mentioned races of closely similar derivation—excepting races 44 and 1—have yielded progenies whose thyroid sizes were more similar than would be expected on the basis of chance alone. Races 50 and 78 have one half of their ancestry in common; the same is true of races 72 and 63a. The two parents of race 67 have three fourths of their ancestry in common. The father and mother of race 62 were unrelated, but three fourths of the ancestry of the mother of this race is also represented in the mother of race 11 (also 11a and 11b); and the father of race 62 is a brother to the mother of O and OT. Other interracial relationships were either absent or of minor degree.

Some further facts concerning the nature and origin of the birds used as the foundation of these races must now be noted. All these birds were of mixed or mongrel composition; a few of them, indeed, contained traces of another genus, though all such were removed by at least four generations from the original cross and contained one sixteenth or less of this different genus. All these races were at least fifteen sixteenths *Streptopelia risoria-alba*. In races 62, 50, 78, 44, 69, 6, 51, NE, 1 and 75 the Oriental turtle dove (*Turtur orientalis*) formed from one

part in thirty-two to one part in two hundred and fifty-six of the ancestry (see Table I). In races 163, OT, 206, 61 and 29 less than one part in sixteen of the ancestry was derived from *Streptopelia douraca;* race NA was about one fourteenth *douraca.* Races 11, 72, O, 67, N2, 63, 63a and 36 are *St. risoria-alba* only. It will be observed that both large and small thyroid races have been established within each of these three main classes of ancestral material.

It may be pointed out that much of this mongrel material, from which it will later appear that we have derived some distinct "thyroid races," is fairly comparable to mongrels attainable within the human family. The blond ring dove (*St. risoria*) and the white (*St. alba*) have often been classed as the same species, and it is wholly probable that they are genetically less different than are the Ethiopian and Caucasian. The Japanese ring dove (*St. douraca*) has once been classed with *risoria,* and the above-mentioned comparison probably holds also for these two forms. Matings of these three kinds of ring doves show *complete* fertility. The Oriental turtle dove is a very distinct form, but it was represented in very small proportion in any race in which it was present at all.

Such diversity of origin as existed in the birds selected for the foundation of our races would of course facilitate the establishment of diverse and distinct endocrine races to whatever extent this diversity supplied different genes for endocrine size. In view of the fact already noted—that both high and low thyroid races have been established in the *St. risoria-alba* material, in which neither *orientalis* nor *douraca* entered—it may perhaps be doubted whether the relatively slight admixture of the latter races really helped our establishment of a thyroid race in any case. Since both *T. orientalis* and *St. douraca* become sexually mature at an older age than does *risoria-alba,* and since the pituitary gland has been found to be intimately associated with age at maturity, it would seem

more probable that the representation of those two species in some of our races would introduce genes having an influence on the pituitary rather than on the thyroid. We may add, however, that at present our work with "pituitary races" does not appear to indicate that either *orientalis* or *douraca* introduced either extreme of pituitary size. There is evidence that the choice of birds showing various types of abnormal reproduction, and the selection subsequently practiced on the progenies of some of these races, were the really effective means of obtaining and establishing these thyroid races. Possibly the usual or frequent choice of two closely related (more nearly homozygous) birds for the foundation of our races was of real importance; it is, however, a fact that our races showing the extremes of thyroid size—in races 62 and 75—were each obtained from a pair of birds not at all closely related.

THYROID SIZE IN TWENTY-FOUR RING DOVE RACES

Table I supplies the principal facts, as these can be presented in summary form, concerning relative and absolute thyroid size in the twenty-four races or strains. The figures given for each race are averages of all healthy individuals of the several generations that have been derived from the parents chosen to found this strain or race. The table shows: (1) the order of thyroid size of each race in relation to all the others—No. 1 having the largest thyroids; (2) the number of healthy birds on which all the averages are based; (3) the name of the race—here, for convenience, sometimes shortened from the name or number originally given; (4) the age, in months; (5) the body weight; (6) the thyroid weight—the sex mean and also the average. It will be observed that the order of thyroid weight is practically the same whether this order is determined by the sex mean or by the average. Race 163 is the marked exception to this rule, and this is a race which was soon lost and includes the smallest number of individuals (only sixteen healthy)

obtained for any race. The three races (72, N2, 63a) having most numerous representatives all show that the sex mean and the average are either identical or practically so. We have used the *average* values in assigning the various races to a fixed position in the tabulated list.

In this assignment of races to a particular position or order in Table I the thyroid size has been corrected for both body weight and age. In general, the body weight does not vary greatly in the different races; and a race (63) with low body weight may be characterized by large thyroids, or a race (61) of high body weight possess thy-

TABLE I

ORDER OF THYROID SIZE IN TWENTY-FOUR RING DOVE RACES

Order	Number healthy birds	Race name	Average age	Weight		
				Body	Thyroid	
					Sex mean	Average
			months	grams	milligrams	
1	87	62	14.8	159	21.9	22.0
2	29	11	14.9	154	18.2	18.2
3	44	50	15.0	159	17.4	17.3
4	156	72	15.1	159	16.9	16.9
5	36	63	13.6	146	15.5	15.6
6	16	163	17.0	160	15.5	16.0
7	32	0	14.1	158	15.3	15.2
8	17	OT	14.7	156	14.8	14.8
9	78	78	13.0	167	15.2	15.2
10	48	67	15.9	167	14.2	14.4
11	38	44	14.1	154	13.5	13.6
12	24	69	13.8	150	13.2	13.0
13	57	NA	17.2	150	13.2	13.1
14	59	6	17.5	144	12.9	12.9
15	71	51	18.2	144	12.9	12.9
16	103	N2	16.7	152	13.1	13.1
17	30	NE	17.6	159	13.5	13.5
18	144	63a	15.8	151	12.8	12.8
19	20	206	10.2	157	13.0	12.9
20	33	1	18.1	155	12.5	12.7
21	48	61	18.6	167	13.0	13.0
22	44	36	13.6	152	12.4	12.4
23	25	29	13.9	149	11.2	11.1
24	78	75	12.1	149	10.9	10.9

roids whose absolute weight is small. Nevertheless, the thyroid weight per 100 grams body weight has been considered in the tabulation. The correction for the age factor, however, has proved a complicated matter, as is indicated by the few following facts: The *mean* values obtained from the five most numerous races (72, 63a, N2, 62 and 72) indicate no change in thyroid size between the ages of seven and seventeen months. Individually, however, these races seem to differ. In races 62 and N2 there is an apparent increase in thyroid weight within these age limits; a decrease is indicated in the other three races. Four of the five races show an increase of thyroid size during the third year. A mean value obtained from these five races indicates that between the ages of seventeen and thirty months the thyroid enlarges to the extent of 0.43 per cent. per month. In general, therefore, the thyroid weights obtained from younger birds are too low and (when older than about twelve months) require a correction for the age factor.

Despite the very considerable variability of thyroid size within each and all of the twenty-four races of Table I, the following kinds of evidence demonstrate a distinction—on the basis of their thyroid size—of the four or five races at the top of the list (Table I) from the four or five races at the bottom of the list. First, the division of the total data for each of these races, on the basis of sex, yields figures which confirm the totals given in Table I. This matter is fully presented elsewhere in a discussion of the relation of thyroid size to sex (Riddle, 1929b). Second, the essential similarity of the average thyroid weight of the several generations of the same race—as this is shown for several races in Tables II, III and IV. Third, by the distribution polygons of Figs. 1 and 2. Fourth, by the fact that in crosses these races definitely tend to transmit the size of thyroid accorded them by the measurements summarized in Table I.

A consideration of the evidence obtained from the behavior of thyroid size in crosses will follow in the next

TABLE II

THYROID SIZE IN EACH GENERATION OF RACES 62, 11, 36 AND 61

	Race	Generation	Parents / Offspring	Number	Group averages: Age	Group averages: Body weight	Group averages: Thyroid weight	Thyroids of parents ♂ and ♀
					months	grams	mgms	mgms
With Large Thyroids	62	F_1	Parents	2	62.1	174	22.7	27.8–17.6
			Offspring	16	14.2	166	20.3	
		F_2	Parents	9	16.7	170	20.9	20.8–20.9
			Offspring	28	12.0	158	21.0	
		F_3	Parents	4	16.9	165	27.4	27.9–27.0
			Offspring	14	17.9	159	24.6	
		F_4	Parents	6	22.0	152	20.4	17.9–22.8
			Offspring	14	15.3	157	24.2	
		F_5	Parents	4	20.6	158	23.2	22.6–23.5
			Offspring	6	11.2	157	18.4	
	11	F_1	Parents	2	92.0	(165)	38.3	49.0–27.6
			Offspring	10	15.9	160	20.2	
		F_2	Parents	8	16.4	159	18.4	17.6–19.1
			Offspring	15	14.9	152	17.4	
		F_3	Parents	6	19.1	148	16.8	16.7–16.9
			Offspring	4	12.9	148	15.7	
	11a	F_1	Parents	2	86.8	(157)	25.6	23.5–27.6
			Offspring	3	39.2	172	22.0	
	11b	F_1	Parents	2	64.3	(165)	20.7	13.8–27.6
			Offspring	6	14.7	165	20.7	
With Small Thyroids	36	F_1	Parents	2	89.8	165	15.0	17.2–12.7
			Offspring	5	16.0	158	12.9	
		F_2	Parents	2	18.0	160	12.1	13.2–10.9
			Offspring	15	13.0	159	11.1	
		F_3	Parents	6	17.9	157	11.6	11.7–11.4
			Offspring	21	10.9	146	13.0	
		F_4	Parents	2	20.0	174	11.8	14.3– 9.3
			Offspring	3	31.4	148	13.3	
	61	F_1	Parents	2	48.9	183	15.0	14.7–15.3
			Offspring	27	18.5	173	13.8	
		F_2	Parents	4	19.8	169	11.0	10.0–12.2
			Offspring	10	21.3	166	12.5	
		F_3	Parents	4	25.0	171	13.0	12.8–13.2
			Offspring	9	17.6	150	11.4	
		F_4	Parents	2	30.0	160	11.0	8.1–13.8
			Offspring	2	10.6	160	11.1	

TABLE III

THYROID SIZE IN EACH GENERATION OF RACES 72 AND 75

Race	Generation	Parents / Offspring	Number	Group averages: Age	Group averages: Body weight	Group averages: Thyroid weight	Thyroids of parents: ♂ and ♀
				months	grams	mgms	mgms
72	F_1	Parents	2	85.8	174	23.5	23.9–23.1
		Offspring	20	16.4	171	16.7	
	F_2	Parents	5	16.6	163	14.6*	14.6–14.6*
		Offspring	13	13.8	158	17.4	
	F_3	Parents	8	15.0	165	19.4	18.5–20.3
		Offspring	30	12.8	157	15.7	
	F_4	Parents	12	18.2	165	15.4	16.5–14.2
		Offspring	43	16.0	156	16.5	
	F_5	Parents	8	20.3	164	15.9	16.8–15.1
		Offspring	28	17.8	158	18.0	
	F_6	Parents	4	25.1	(152)	17.8	18.3–17.3
		Offspring	2	17.6	157	18.1	
72 Back-cross F_1 ♂ and mother	F_1	Parents	2	53.5	181	19.4	15.6–23.1
		Offspring	3	13.1	157	18.7	
	F_2	Parents	2	14.5	169	19.4	17.0–21.8
		Offspring	9	12.5	158	18.2	
	F_3	Parents	4	17.2	165	20.9	23.2–18.6
		Offspring	8	12.6	151	16.9	
75	F_1	Parents	2	28.9	151	9.4	11.2– 7.5
		Offspring	15	14.8	153	13.0	
	F_2	Parents	10	14.3	153	12.8	13.4–12.1
		Offspring	26	13.8	153	9.8	
	F_3	Parents	14	18.2	150	10.2	10.0–10.4
		Offspring	26	7.6	145	10.7	
	F_4	Parents	2	10.1	161	12.6	14.1–11.0
		Offspring	1	4.7	130	9.2	
75 Back-cross	F_1	Parents	2	26.2	135	12.5	11.2–13.7
		Offspring	6	15.0	146	11.0	
	F_2	Parents	2	23.3	143	8.5	9.5– 7.5
		Offspring	4	18.2	154	11.7	

* One female thyroidectomized when young regenerated 9.9 mgm thyroid.

TABLE IV

THYROID SIZE IN EACH GENERATION OF RACES 63a AND 63

Race	Generation	Parents Offspring	Number	Group averages			Thyroids of parents
				Age	Body weight	Thyroid weight	♂ and ♀
				months	grams	mgms	mgms
63a	F_1	Parents	2	89.0	163	18.8	22.3–15.3
		Offspring	2	14.4	157	14.7	
	F_2	Parents	2	14.4	157	14.7	13.2–16.2
		Offspring	10	14.4	151	16.4	
	F_3	Parents	2	20.6	156	14.5	16.7–12.3
		Offspring	6	12.7	156	13.5	
63a Back-cross F_1 ♂ and mother	F_1	Parents	2	54.3	165	15.2	15.0–15.3
		Offspring	10	15.9	158	13.4	
	F_2	Parents	6	13.8	158	14.9	14.9–14.8
		Offspring	12	14.5	152	11.7	
	F_3	Parents	6	17.0	154	12.2	12.2–12.3
		Offspring	22	18.0	158	12.1	
	F_4	Parents	14	19.5	160	12.1	12.4–11.1
		Offspring	46	17.4	149	12.3	
	F_5	Parents	14	19.9	150	11.8	11.8–11.8
		Offspring	33	13.5	147	12.9	
	F_6	Parents	2	16.4	146	12.7	15.8– 9.6
		Offspring	3	18.0	150	12.8	
63	F_1	Parents	2	88.2	160	32.2	49.0–15.3
		Offspring	6	10.2	142	17.6	
	F_2	Parents	6	9.4	141	19.4	22.5–16.3
		Offspring	12	12.9	150	14.0	
	F_3	Parents	4	17.0	150	11.5	11.1–12.0
		Offspring	13	15.2	145	16.2	
	F_4	Parents	2	20.0	149	16.4	8.4–24.4
		Offspring	5	15.2	143	15.5	

section of this paper. Two other kinds of evidence require a further statement here. In Tables II and III some "large thyroid" and some "small thyroid" races are so grouped as to make evident the distinctions of thyroid size in all the several generations thus far obtained. These tabulations (also Table III) show that not

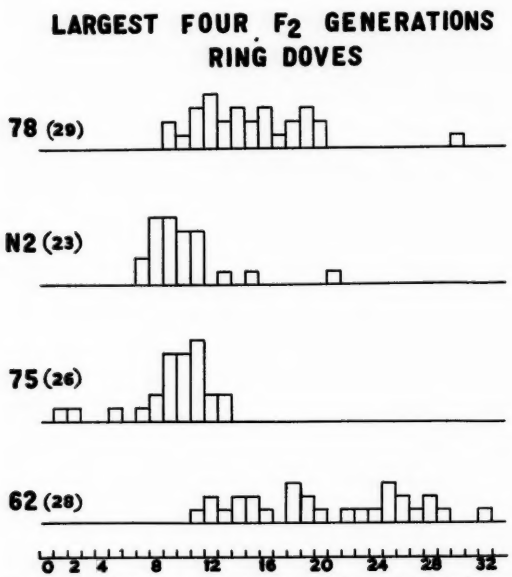

FIG. 1. Showing distribution of thyroid weights of individuals of four first (one polygon showing second) generations.

merely a final average, but also the separate averages obtained for the offspring of each generation, are in fair agreement as to the characteristic thyroid size of each race. In Table III a back-cross in a race (72) with large thyroids also yielded large thyroids in three successive generations; in a back-cross within a "small thyroid" race (75) we obtained two generations showing small thyroids. In Table IV are shown the results of mating the same female to three different males. Thyroids of intermediate and rather irregular size were obtained from the first mating. From a second mating, made with a son (F_1 of above mating), small thyroids were obtained in each of six generations. The third mating of this female was made with a male closely related to the birds which founded race 11—a race with large thyroids. From this mating thyroids of large or of intermediate size were obtained in four generations.

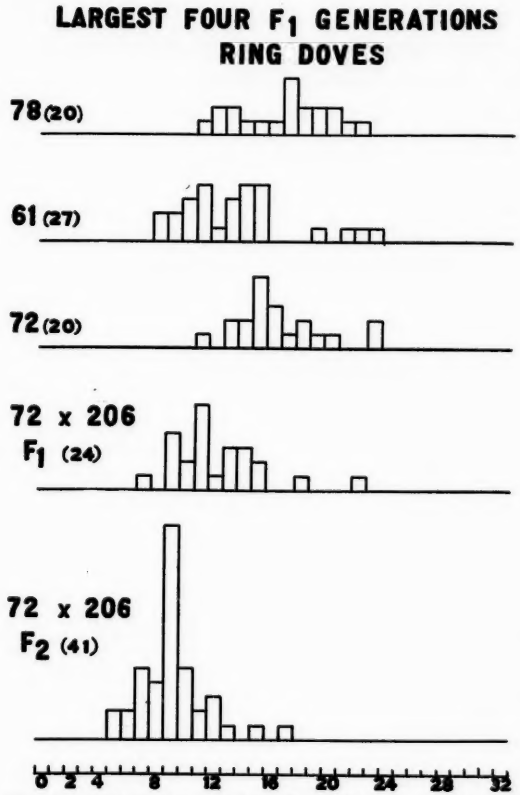

FIG. 2. Showing distribution of thyroid weights of a first generation in four races.

Figs. 1 and 2 show the distribution of thyroid weights obtained for certain races in generations F_1 and F_2. These polygons show the variability of these thyroid weights, and they also support other evidence that such races as 75 and 62 are characterized by distinctly different thyroid size.

THE INHERITANCE OF THYROID SIZE

The behavior of thyroid size in hybridization is adequately shown by the data of Tables V and VI, and the

results require little comment. The races used in these crosses are, of course, those listed in Table I. At the top of Table V are placed, in order, the four races with largest thyroids—together with all the crosses made with these races. When each of these "large thyroid" races was crossed with another "large thyroid" race it is evident that the resulting F_1, F_2 and F_3 hybrids were characterized by large thyroids. Also, when races characterized by small thyroids were crossed with other "small thyroid" races the resulting hybrids of the various generations have thyroids of small size.

In Table V are grouped all the crosses that have been made with six races which appear to have thyroids of intermediate size. Here, too, it is evident that when such races are mated with either of the four "large thyroid" races the resulting hybrids invariably (as groups) have larger thyroids than those of the intermediate race used in the cross. The table affords eight such tests for F_1; four for F_2; one for F_3. When these same (intermediate) races were mated with either of the four "small thyroid" races the resulting hybrids had smaller thyroids than those of the "intermediate" race in six of the eight tests made. Indeed, Table VI indicates that the order of thyroid size within the twenty-four races, as this was determined in Table I, is essentially the same order in which these races influence thyroid size in hybridization. Thus the racial differences found by one method in Table I are nicely confirmed by tests of the behavior of those differences in crossing.

The available data do not indicate the number of genetic factors which condition thyroid size. The variability of this organ is so great (Figs. 1 and 2) that much larger numbers of F_2 individuals from certain crosses are required for a solution of that problem. The data of Tables I, V and VI suggest, however, that more than one such factor is involved. The present data also provide no definite answer to the question of dominance or recessiveness of large thyroid. Possibly our consideration of

TABLE V

THE INHERITANCE OF THYROID SIZE IN ALL CROSSES MADE OF LARGEST (4) AND SMALLEST (4) "THYROID RACES" WITH OTHER RACES WHOSE THYROID SIZE WAS KNOWN

Race × Race					Thyroid weight in generations:					
					F_1		F_2		F_3	
Name of race	Thyroid weight		Name of race	Thyroid weight	Weight	Number	Weight	Number	Weight	Number
	mgms			mgms	mgms		mgms		mgms	
62	22.0	×	11	18.2	23.1	4	22.2	9	19.6	4
			N2	13.1	16.9	13	19.5	3		
			63a	12.8	20.9	10	16.0	7		
			36	12.4	16.4	9	13.5	2		
11	18.2	×	62	22.0	23.1	4	22.2	9	19.6	4
			72	16.9	27.1	4				
			63a	12.8	17.3	9	16.0	7		
			1	12.7	21.3	5				
50	17.3	×	163	16.0	17.6	11	26.7	22		
72	16.9	×	11	18.2	27.1	4				
			0	15.2	13.5	9	12.1	2		
			OT	14.8	16.2	6	14.0	11	14.2	3
			44	13.6	14.9	10	14.7	6	17.6	2
			69	13.0	15.1	4				
			51	12.9	16.0	9	16.1	4		
			NE	13.5	12.1	12	11.6	10		
			63a	12.8	16.5	20	12.6	2		
			206	12.9	12.6*	24	9.7*	41	10.6*	17
			61	13.0	17.9	11	13.0	1		
			36	12.4	12.7	4				
61	13.0	×	11a	22.0	15.6	7	18.5	6	19.3**	5
			72	16.9	17.9	11	13.0	1		
			44	13.6	11.8	2	18.7	3		
			63a	13.0	12.1	9				
			1	12.7	12.1	13	13.6	14		
			29	11.1	9.7	7	10.5	21	14.7	6
36	12.4	×	62	22.0	16.4	9	13.5	2		
			72	16.8	12.7	4				
			N2	13.1	9.9	2				
			63a	12.8	10.8	1				
29	11.1	×	69	13.0	12.0	4				
			61	13.0	9.7	7	10.5	21	14.7	6
75	10.9	×	no crosses							

* Two F_1 birds with thyroids unusually small for their respective races (72 = 13.7; 206 = 11.7) were used as parents in this cross.

** A weight of 24.6 mgms was obtained for three F_4 offspring.

TABLE VI

THE BEHAVIOR OF THYROID SIZE IN ALL CROSSES MADE WITH SIX RACES CHARACTERIZED BY THYROIDS OF INTERMEDIATE SIZE

Race × Race					Thyroid weight in generations:					
					F_1		F_2		F_3	
Name of race	Thyroid weight		Name of race	Thyroid weight	Weight	Number	Weight	Number	Weight	Number
	mgms			mgms	mgms		mgms		mgms	
44	13.6	×	72	16.9	14.9	10	14.7	6	17.6	2
			N2	13.1	13.5	12	17.3	21	13.2	8
			63a	12.8	17.0	7				
			61	13.0	11.8	2	18.7	3		
51	13.3	×	72	16.9	16.0	9	16.1	4		
			6	12.9	10.9	4	9.7	4		
			1	12.7	13.8	17	12.0	16	12.8	18
69	13.0	×	72	16.9	15.1	4				
			29	11.1	12.0	4				
N2	13.4	×	62	22.0	16.9	13	19.5	3		
			OT	14.8	13.2	9	13.8	12		
			44	13.6	13.5	12	17.3	21	13.2	8
			NE	13.5	11.2	3				
			63a	12.8	14.2	13	14.1	14	8.4	3
			36	12.4	9.9	2				
63a	12.8	×	62	22.0	20.9	10	16.0	7		
			11	18.2	17.3	9	16.0	7		
			72	16.9	16.5	20	12.6	2		
			44	13.6	17.0	7				
			N2	13.1	14.2	13	14.1	14	8.4	3
			NE	13.5	14.5	20	12.6	2		
			61	13.0	12.1	9				
			36	12.4	10.8	1				
1	12.7		11	18.2	21.3	5				
			51	12.9	13.8	17	12.0	16	12.8	18
			61	13.0	12.1	13	13.7	15		

this matter should await the results of current studies whose purpose is to determine which of our "large thyroid" races have hypo- and which have hyper-functioning thyroids. Certainly any valuable consideration of this point must await the accumulation of further data from many additional crosses, particularly from those involving "large thyroid" and "small thyroid" races.

The details of our data make it quite clear that thyroid size in this material is neither a sex-limited nor a sex-linked character. Such details are involved incidentally in another publication (Riddle, 1929b) and will be little considered here. It was there shown that thyroid size is very nearly equal in the sexes. In the twenty-four races of Table I, with thyroid calculated on the basis of 100 grams body weight, thyroid weight in the females (682) exceeds that of the males (635) by a racial mean of only 4.5 per cent.; and similar data for the twenty-two most numerous kinds of hybrids (Tables V and VI) show an excess of only 1.8 per cent. Further, this slight excess is probably fully accounted for by temporary enlargement of the female thyroid at reproductive periods, and by the greater ease with which the female thyroid undergoes hyperplasia (endemic goiter) as a response to several physiological factors.

Discussion

If exophthalmic goiter has appeared in this material the advanced cases of it at least would probably have been accompanied by emaciation or other sign of disease which would eliminate such thyroids from all our averages—excepting only those for "parents," as given in Tables II, III and IV. In these latter cases thyroid weight is recorded for birds dead of disease, and thyroids from diseased birds show a higher average weight than do those from healthy birds. This circumstance—together with the fact that birds used as parents average older than the non-parents—explains the tendency (Tables II, III, IV) of the thyroids of "parents" to be larger than those of their offspring. It is not certain, however, that no races with hyper-functioning thyroids are included among the several races having unusually large thyroids. This point, and others involving the basal metabolism of all these races, is now being studied in collaboration with Dr. F. G. Benedict, of the Nutrition Laboratory, Boston.

This study of inheritance deals with the weight of an organ which is wholly invisible during life, and it is necessary to indicate how this was accomplished. It is clear that in many cases one or both of the birds selected for the foundation of a "thyroid" race already possessed the sort of genetic constitution that we were seeking; that is, one or both of the birds carried genes which predispose to large or to small thyroid size. It is highly probable that our utilization of the reproductive records of these birds greatly facilitated success in obtaining at the outset these extremes of thyroid size. The evidence for this is of several kinds, but we shall here note only that precisely those races which show extremes of thyroid size have proved, despite the special efforts centered upon them, to be most difficult to propagate. Races 11, 50, 163, NE and 206 have been lost entirely (except as hybrids), and races 62, 75, 29, 36 and 61 have been maintained only with difficulty. On the other hand, most of the races having thyroids of intermediate size (excepting some involved in selection for extremes of pituitary size) continue to show better reproduction and greater ease of propagation.

The establishment of some of these races was further assisted by the selection of particular fraternities or progenies for continued breeding and by the elimination of certain fraternities from further breeding. In our work with the thyroid (exclusive of pituitary) this selection was practiced on only eight of the twenty-four races. Those races are the four which now stand at the top and the four now found at the bottom of Table I. This selection was almost entirely confined to F_1 and F_2, and was accomplished in the following manner: Two to five pairs of a particular (F_1) progeny were permitted to produce young; then, after all or most of the parents had been killed and the size of their thyroids was known, some among these progenies were listed for further breeding and some for killing without further breeding. When selecting for a "large thyroid" race this further breeding

was restricted to offspring of that pair of parents which was found to have the largest thyroids. That this selection was effective is illustrated by the data given for races 72 and 75 in Table III. In back-crosses no selection was practiced in any case.

The specially gratifying result of this study is that we now have at hand a supply of individuals in which thyroid size, and presumably thyroid function, is standardized. This material is therefore specially suitable for use in the solution of several medical and biological problems. Aside from some obvious abnormalities in reproduction, no conclusions have yet been drawn concerning the correlation of one or another physical characteristic with these racial differences in thyroid size. This will be done later, and the results should notably assist the interpretation of the relation of grades of thyroid function to certain physical traits in man.

Summary

Within a large colony of ring doves, mongrelized to a degree fairly comparable with that attained or attainable in mankind, physiological factors influencing thyroid weight have been controlled to an extent which has made possible a demonstration of genetic factors for thyroid size.

Twenty-four strains or races have been studied, and at least four races with characteristically large thyroids and four races with characteristically small thyroids have been definitely established. This is the first demonstrated instance of the conscious establishment of a race on the basis of size or function of an endocrine gland.

The surviving individuals of these races probably represent the nearest approach yet made to a biological standardization of an organism on the basis of thyroid size and function. This material is therefore specially suitable for the solution of a wide variety of biological problems. Ultimately it should particularly assist an in-

terpretation of the relation of grades of thyroid function to certain physical traits in man.

The attainment of this result was probably assisted by the choice of birds showing various types of reproductive disorder as the parental stock with which to initiate some of these races. A further selection for large or for small thyroid was practiced among progenies of the F_1 and F_2 generations.

Crosses were made between races of all types—large, intermediate and small. Considering merely the average thyroid weight within each generation the results are as follows: Large thyroid $\times$ large thyroid has given large thyroid in F_1, F_2 and F_3. Small $\times$ small gives small thyroids in F_1, F_2 and (partly) F_3. Intermediate $\times$ intermediate tends (not always) to give intermediate in F_1, F_2 and F_3. Apparently, large $\times$ small yields thyroids of intermediate size in F_1, F_2 and F_3.

Questions of dominance, and of the number of genetic factors involved in thyroid size, must await the further accumulation of data from certain crosses. There is no suggestion of sex-limited inheritance of thyroid size in this material. The study is based on the thyroid weights of 1,931 healthy adult offspring of fifty parental ring doves whose thyroid size was also known.

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THE CONTRACTILITY OF PROTOPLASM[1]

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CONTRACTILITY, elasticity, cohesiveness, rigidity and tensile strength are closely related properties of living matter which owe their existence to a specific type of structure. Polarity and conductance are other properties of protoplasm which, though of quite a different nature from those first enumerated, depend upon the same specific structure.

It is my purpose to give experimental proof of the presence of these physical properties in protoplasm and then to consider the character and arrangement of the structural units which account for these properties.

I have already presented to this society[2] a general idea of a structure which meets the requirements of an elastic yet fluid system. It is my wish to-day to carry this concept still further and to give a more detailed picture of the architectural background of protoplasm.

The earliest investigators of living matter realized that the substratum of life has certain properties which are more characteristic of solids than of liquids. Pfeffer deserves credit for making the first quantitative measurement of one of these properties. He performed the ingenious experiment of tying minute weights to the end of a freely hanging strand of the plasmodium of the slime-mould Chondrioderma and ascertaining the load which the protoplasmic thread would support. From this he calculated the tensile strength or, as he expressed it, the cohesive force of the protoplasm. (This was found to average 50 mgr per sq. mm; 3.5 mgr actual weight on a strand measuring 0.3 mm in diameter.)

The modern technique of microdissection (termed "Micrurgie" by Péterfi) has given us another way to

[1] Address given at the Symposium on "The Neuromuscular System," American Society of Naturalists, New York City, December 29, 1928.

[2] AMER. NAT., 60: 124 (1926).

demonstrate, and to measure with accuracy, certain of the physical properties of protoplasm. Stretching the living substance between microneedles will convince any one of its extraordinarily high elasticity and tensile strength. Those workers who repeatedly emphasize a liquid nature of protoplasm should go through the experience of placing microneedles in a red blood corpuscle and stretching this corpuscle to its elastic limit (Fig.

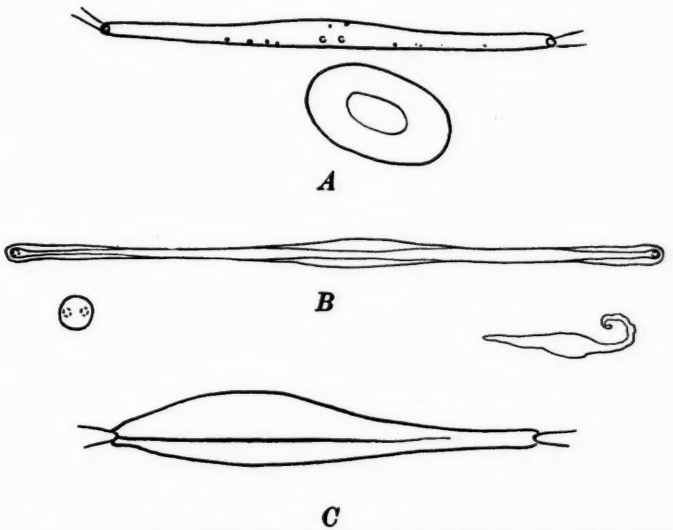

FIG. 1. *A*. An erythrocyte (from the amphibian Cryptobranchus) stretched between microneedles. (A normal corpuscle is just below.) *B*. The isolated nucleus of an amphibian (Cryptobranchus) erythrocyte, before stretching (14 μ dia.), stretched (to over 300 μ), and after contracting to near its original size. *C*. The stretched isolated nucleus of Amoeba. (*A* and *C* are from photomicrographs.)

1, A): of putting two fine needles into the nucleus of an amphibian erythrocyte (Fig. 1, B), or of an Amoeba (Fig. 1, C), and stretching the nuclear substance to near its breaking point, and then see the nucleoplasm suddenly contract to almost its original size when the needles are removed (Fig. 1, B).

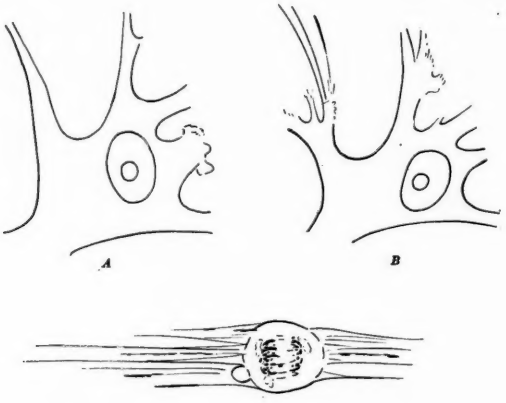

FIG. 2. Cells from the Carrel cinématograph. *A*. Rat sarcoma fibroblast in culture, before contraction. *B*. The same after contraction of the upper left pseudopod and the formation of long tenuous protoplasmic threads. *C*. Chick embryo fibroblast about to undergo division (chromosomes approaching the poles) showing exceedingly long protoplasmic processes.

The application of the cinématograph to biological studies has made it possible to better visualize many behavior phenomena in living matter. The extraordinarily rapid contraction of protoplasmic strands formed by cell growth in tissue-cultures becomes, when depicted by moving pictures, impressive evidence of the high contractility of protoplasm. One can not adequately describe this phenomenon. It must be seen to be appreciated.

Through the courtesy of Dr. Alexis Carrel I was able to show, at the symposium, a cinématograph of tissue-culture cells. Here I can give only sketches of those cells which possess long protoplasmic processes of such extraordinary contractility and tensile strength. Fig. 2, A, B, C, gives three outline copies of cells in the Carrel moving picture.

Fig. 2 illustrates a cell (A) before and (B) after the contraction of a large pseudopodium (upper left corner)

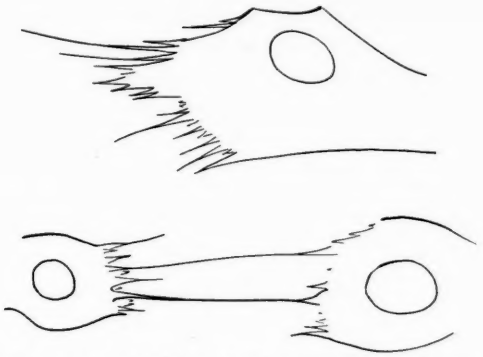

FIG. 3. Cells from normal thick embryo heart cultures showing protoplasmic processes.

which leaves in its track numerous exceedingly slender and taut protoplasmic threads that snap back to the cell surface with marked suddenness when torn from their points of contact. The protoplasmic strands illustrated in Fig. 2, C, are formed by a dividing cell just prior to actual division of the cytoplasm. (The chromosomes are to be seen moving to the poles.) Fig. 3 (from my own cultures of chick embryo heart) gives other examples of long, tenuous, tightly stretched protoplasmic processes of cells in tissue-culture.

We see, therefore, that protoplasm is highly contractile and elastic, and possesses a measurable tensile strength. While these properties are more pronounced in protoplasm in the firm condition, they are also typical of living matter when it is quite fluid. The properties of solids characterize protoplasm, and this is true even when the living substance is of low viscosity and possesses other properties typical of the liquid state such as the capacity to flow. There is nothing incongruous or contrary to ordinary concepts of the properties of matter in the assertion that protoplasm possesses both liquid and solid properties, for it belongs to that group of substances, the jellies, which are intermediate between what is usually regarded as solid and as liquid.

Polarity and electrical conductance are other properties of living matter which point to the same type of structural basis as do the contractile and elastic qualities.

Polarity is a property of things which is of wide occurrence in nature. It is an expression of the systematic arrangement of molecules and of molecular aggregates.

Unquestionably one of the most fundamental laws of nature is the inevitable tendency of all things to orient themselves. Even liquids in solution yield diffraction patterns indicative of some kind of arrangement, and these patterns permit the calculation of the distance of nearest approach of molecules even when in thermal agitation.

Magnetism is a classical case of polarity. It is due to the adjustment of iron crystallites whose orientation is the structural basis of magnetism. The sound caused by the rearrangement of the particles can now actually be heard. The phenomenon is known as the Barkhausen[3] effect. The magnetization of iron causes a sudden reorientation of groups or chains of molecular magnets which produces a noise that is audible when amplified. The softer the iron the greater is the noise. Hardened steel yields no noise. It is a noteworthy scientific achievement that the sound of this movement can be made audible.

Electrical conductivity is the last of the physical properties of protoplasm to which I wish to refer. It has, I believe, a very direct bearing on the problem at hand, namely, the structural background of the living substance. Conductance is especially characteristic of that part of organisms which is the subject of this symposium, namely, the neurofibrils.

The precise nature of conductance in living fibrils is not with certainty known. The present tendency is to regard all forms of stimulation as electrical. It is further thought that the excitation-wave travels over the cell

[3] *Phys. Zeitschr.*, 20: 401 (1919); see also Tyndall, *Phys. Rev.*, 24: 439 (1924).

surface, and is, therefore, essentially a membrane phenomenon. The fact in which we are here primarily interested is that electric currents travel with great speed along nerve fibers. The same is true of metals known as conductors. Among these occur some interesting variations in ease and rate of conduction.

Properly annealed copper conducts electricity much better than ordinary copper or the same copper after it has been struck by a hammer.[4]

Copper of a single crystal should have a conductivity 14 per cent. greater than ordinary copper along one axis. Slow cooling gives the atoms time to arrange themselves as they wish, and they prefer to build up a single crystal rather than a multitude of small ones. In the growth of a large crystal the atoms arrange themselves in columns along the length of the crystal. It is this regular and linear arrangement which gives to single crystals their superior conductivity. There is reason to believe that the increased conductivity of crystalline copper along a certain axis should be as much as 60 per cent. over the value of ordinary copper, but this increased conductivity must be along an axis in the direction of which crystals can not be made to grow under controlled experimental conditions. If a large-sized crystal of copper of high conductivity is hammered, filed, or bent, the conductivity is reduced to that of ordinary copper. The linear and orderly arrangement of the atoms has been disturbed; it is now chaotic.

Crystals show similar properties in regard to conduction. Heat and light are transmitted more quickly in one direction than another. A simple experiment can be performed to show that heat conductance in a crystal is not the same in all directions. If calcite is coated with paraffin and a hot needle touched to the surface, the paraffin melts within an area which assumes an oval shape. If this experiment is done on the surface of rock salt, the melted area is circular, that is, the rate of travel of heat

[4] G. Bartlett, *J. Chem. Ed.*, 4: 822 (1927).

in the sodium chloride crystal is the same in all directions, which is not true for calcite.

The basic crystalline unit of common salt is the cube. The elementary space lattice of calcite is the rhombohedron. In the former, all axes in the crystal are alike: in the latter, a wave traveling along one axis would have a different path to follow than along another axis; in other words, the NaCl crystal is isotropic, *i.e.*, has properties equal in all directions, while the $CaCO_3$ crystal is anisotropic, with properties varying along different axes.

To what conclusion do these observations lead? They indicate that in all systems which exhibit contractility and related properties, which possess polarity and the capacity for efficient conductance, the basic structural unit is a linear one.

We have not seen the ultimate unit of living matter, we may never see it, directly or indirectly, since it is of molecular dimension, but we have seen structural features in protoplasm which are expressions of the basic unit. The cytologist is familiar with many of these. We shall refer to some later.

Any attempt to give a picture of the shape of the linear structural units which build up the substratum of life is going to be in the nature of a speculation based on analogy. Only by comparing living matter with those non-living systems which possess the same physical properties that characterize protoplasm can we hope to obtain even a remote idea of the molecular architecture of protoplasm.

Among the non-living systems the proteins are the ones to which we should naturally turn for comparison with protoplasm, since they are the chief constituents of living matter. Pauli[5] has expressed this view-point in saying:

> It would be superfluous to discuss which of the constituents of the living cell are most important in vital processes. Proteins, lipoids, and certain inorganic salts are alike indispensable and have a very intimate relation, both

[5] "Colloid Chemistry of the Proteins" (Trans. Thorne), London, 1922.

physical and chemical, one to another. There is, however, no doubt as to the central position of the proteins in the organization of living matter. Apparently they occur in nature in close connection with vital processes; in the living cell they are completely irreplaceable; and, above all, they alone display the specific properties of living matter. In consequence the distinctions observed, not only between different kinds of organisms but even between individuals of the same kind, reappear on chemical investigation as variations in the respective proteins.

One could indulge in interesting speculation on the structure of the protein molecule. Its basic unit, the amino acid, is of the desired linear type. But it is another substance which is to serve for comparison with protoplasm in the present article. This substance is cellulose. Though belonging to a different chemical group from the proteins, cellulose is very much like them in certain of its physical, especially colloidal, properties. Recent investigations on the structure of cellulose suggest the probable type of architecture which lies hidden in the optically homogeneous matrix of protoplasm.

Meyer and Mark[6,7] have made a comprehensive and critical study of results obtained chiefly by others on the structure of cellulose.[8] The present article deals primarily with their interpretations, but it should be understood that the structure which they propose is based very largely on the conclusions of organic chemists (Irvine,[9] and others), conclusions which are, in the main, supported by X-ray evidence or at least are not inconsistent with X-ray patterns.

The structural unit of cellulose is a "glucose residue." Its formula is $C_6H_{10}O_5$. "Residue" is not used here in the orthodox sense. The "glucose residue" is anhydrous glucose, and has, therefore, an obvious stoichiometrical relationship to glucose.

The glucose residue consists of a typical carbon ring of five carbon atoms and one oxygen atom. Joined to such

[6] K. H. Meyer and H. Mark, *Ber. deutsch. chem. Gesell.*, 61: 593 (1928).

[7] K. H. Meyer, *Die Naturwissenschaften*, 16: 781 (1928).

[8] I am much indebted to Dr. A. W. Kenney and Dr. W. H. Carothers, of the du Pont Experimental Station, for their kind assistance in the interpretation of work done on cellulose structure and for added information.

[9] *J. Chem. Soc.*, 123: 525 (1923).

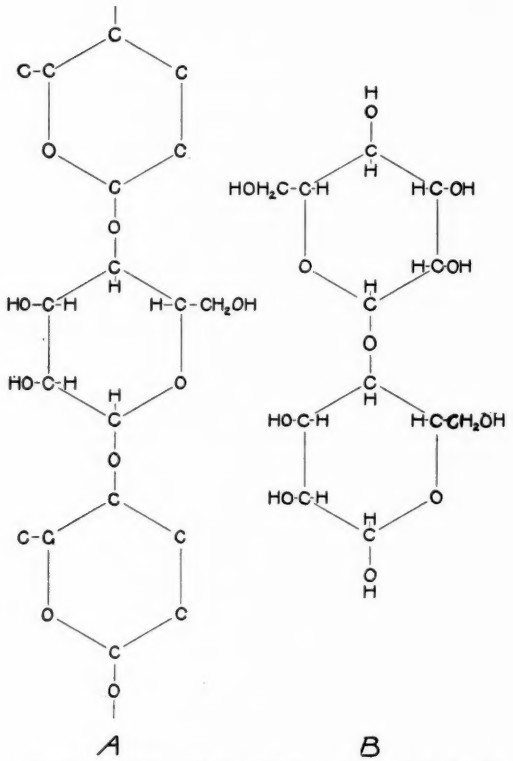

FIG. 4. *A*. Three "glucose residue" units (one and one half links) of a cellulose chain. *B*. A molecule of cellobiose.

a ring—by an oxygen bridge, the bond being between carbons 1 and 4—is another ring which is the reflected image of the first, that is, it is rotated through 180°. These two units, taken as a pair, constitute one link in the cellulose chain. The structural formula of a link and a half, *i.e.*, of three glucose residues, is given in the accompanying Fig. 4, A. By repeating this link some twenty times (forty glucose residues) we arrive at the structure which constitutes a cellulose chain. This is the nearest approach to that which can be regarded as a cellulose molecule.

A moment's study of the formula of a link reveals the fact that it is really the simple sugar, cellobiose, minus water. The structural formula for cellobiose is given in Fig. 4, B. This is a perfectly definite compound of fixed molecular weight.

The length of a cellulose chain is not fixed. It is capable, stoichiometrically at least, of reaching any length. One can not, therefore, speak of a cellulose molecule in the strict sense. The molecule as a definite and fixed thing does not exist, that is, its size can not be ascertained with certainty.

Sponsler and Dore,[10] on the basis of X-ray studies, have reached conclusions which are in certain respects similar to those set forth here. They were among the first X-ray workers to emphasize the long chain structure. The arrangement of the atoms suggested by Sponsler and Dore differs somewhat from that generally held. These investigators regard cellulose as made up of glucose units of which the amylene oxide ring formula is in closest agreement with X-ray requirements. The units are united in chains of indefinite length. Sponsler and Dore conclude that "the proposed structure accounts for the tensile strength of the (ramie) fibers in the longitudinal direction. It also explains the different longitudinal and lateral thermal expansions, and accounts for swelling phenomena."

Chemical analyses lend support to the hypothesis that the unit of the cellulose molecule is glucose in a modified form. Cellulose yields glucose by hydrolysis when dissolved in 41 per cent. hydrochloric acid.[11] Irvine and Hirst,[12] using alcoholic HCl, brought the yield of glucose to 95.1 per cent. of that demanded by the expression $(C_6H_{10}O_5)_x \rightarrow C_6H_{12}O_6$.

Chemical analyses of cellulose bring up the question of the disposition of the unsatisfied valence bond at the end

[10] Colloid Symposium Monograph, IV, New York, 1926.

[11] R. Willstätter and L. Zechmeister, *Ber. deutsch. chem. Gesell.*, 46: 2401 (1913).

[12] *J. Chem. Soc.*, 121: 1585 (1922).

of the chain. One chemist has answered the question by saying that the free valence indicates not an actual free carbon bond but the place where our knowledge ends.

Some disposition must be made of the valences at the end of the chains. Three possibilities appear: the valences may be free, they may be saturated by univalent groups, or they may be united with the formation of a ring. The first of these possibilities seems very improbable, though Staudinger[13] has at one time favored the view. It is difficult to distinguish experimentally between the remaining two possibilities, that is, by analysis between a compound having a formula $(C_6H_{10}O_5)_{40} \cdot H_2O$ and a compound having the formula $(C_6H_{10}O_5)_{40}$. If cellulose has the first formula, then there are hydroxyl groups at the end of the chain which are absent in the second formula. It might be possible to prove their presence by the formation of certain derivatives. Thus, cellulose on methylation yields trimethyl cellulose and this can be hydrolized to trimethyl glucose, which can be identified. If a molecule having the first formula were methylated and then hydrolized, there would be formed thirty-nine molecules of trimethyl glucose and one molecule of tetramethyl glucose per molecule of cellulose. Work done in this field leads to the conclusion, not that the hydroxyl groups are absent from the ends of the chain, but simply that the chain is so long that the relative amount of tetramethyl glucose formed is too small for detection.

There are, as will be pointed out in more detail later, many polymeric materials which are constituted on the same principle as cellulose, that is, their molecules are characterized by a recurring structural unit. One of the simplest possible polymers of this general type is found in the polyoxy-methylenes. The structure of these has been thoroughly established by Staudinger, and the structural unit found to be $-CH_2O-$. The question of the disposition of the valence at the end of the chains in the

[13] *Ber. deutsch. chem. Gesell.*, 59: 3019 (1926).

polyoxy-methylenes has been decided. These valences are satisfied by univalent groups from water, sulfuric acid, or methyl alcohol, depending on the method by which the polyoxy-methylene is prepared. It seems probable that all linear polymers are open chains and that the end valences are satisfied by univalent groups, although it has been argued that the valences at the end of the chain in rubber and in some synthetic hydrocarbon polymers are united to form large rings. Other work on synthetic polymers has established pretty definitely that these polymers are not large rings, but open chains, some of which have hydroxyl groups at the ends, others carboxyl groups, and still others have halogens. The presence of the halogens can be detected analytically and the carboxyl groups by titration with alkali. The presence of hydroxyl groups is difficult to detect.

The cellulose chains are aggregated into bundles. The bundle consists of some fifty to sixty closely packed parallel chains. To such a fascicle Meyer and Mark have given the old Nägeli term "micella." The arrangement of the chains is orderly (Fig. 5). The elementary space lattice is either rhombic or monoclinic. The balance of evidence appears to favor the latter structure with the acute angle close to 90°. Regular arrangement of particles characterizes the crystalline state. Since such a condition exists in cellulose fascicles they are termed crystallites.

The distribution of the micellae in a mass of cellulose has been compared to that of bricks in a wall, but such regularity would make cellulose distinctly crystalline in all its properties, which is not true. In this connection it is important to point out that even purified cellulose probably does not consist entirely of crystallites. The title of Meyer and Mark's[6] article emphasizes this aspect when they refer to the "crystalline portion" of cellulose. The nature of the cementing material is not definitely known. The orientation of the crystallites is confined to the fact that the long axes are approximately parallel;

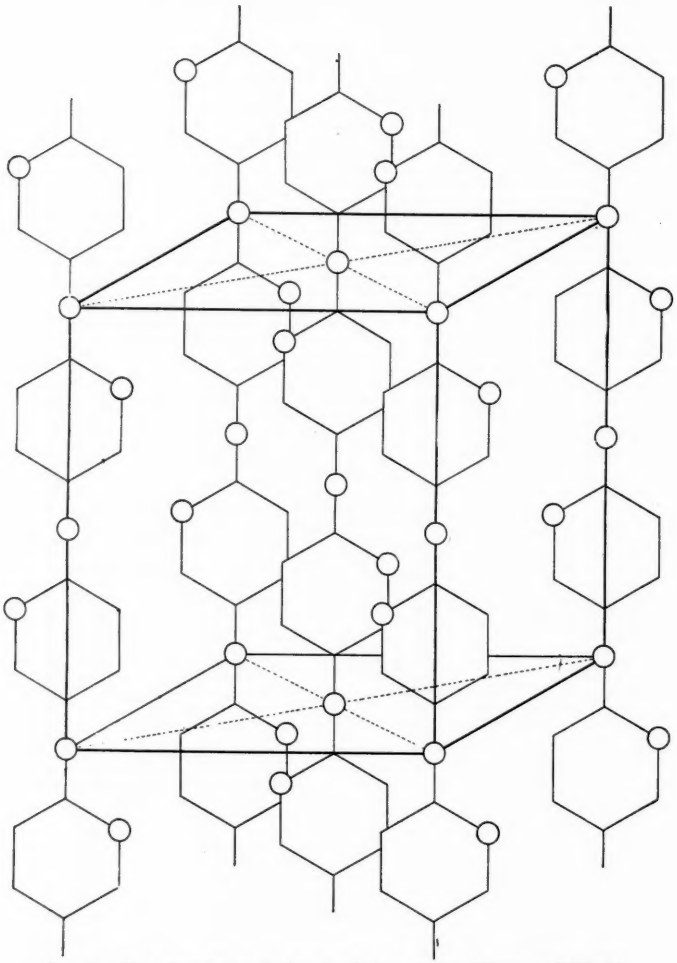

FIG. 5. The elementary body of cellulose (after Meyer and Mark).

aside from that, they may have any position or orientation and decidedly lack the regularity of bricks in a wall.

Any attempt to graphically represent the links, chains and micellae in a block of cellulose, while accurate in part, is going to necessitate the addition of details which we really know little or nothing about. Fig. 6 is such an

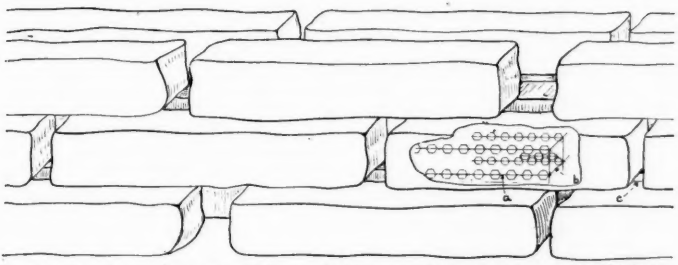

FIG. 6. A number of cellulose micellae, the interior of one of which is, in part, exposed and enlarged to show the chains of glucose residue units: *a* = primary valency forces, *b* = secondary association forces, *c* = tertiary micellar forces.

attempt and should be regarded as approaching accuracy in so far as it indicates that the chains are of different lengths, that the crystallite has an internal arrangement of chains which is orderly, that it is very long compared with its diameter and that its position is random except that the long axes of the crystallites are parallel.

The forces which hold the units of a chain together are primary valence ones. Those which hold the chains together in a bundle are of a secondary type. There must also exist residual surface forces which tie the micellae one to another in a block of cellulose. These are of a tertiary nature and must be capable of considerable adjustment since they are firm in a xerogel, less firm in an elastic jelly and loose in a liquid cellulose dispersion which though it flows smoothly yet retains some elasticity. Herzog[14] states that in many cases a number of micellae come together to build up larger structural units which he calls secondary particles. If this is true then we are dealing with forces of still another and weaker order of magnitude.

The naming of the several types of forces which hold the links, chains and micellae together is somewhat arbitrary with each worker. Wise[9] regards intramicellar forces as primary and intermicellar ones as secondary,

[14] *Z. angew. Chem.*, 34: 385 (1921).

while Meyer[7] states that the glucose residues are bound together by primary valence forces to form chains which can, therefore, be termed "primary valence chains," and these, in turn, are held together by "association" or "micellar" forces to form crystallites.

We can state with certainty that the forces with which we are dealing are of at least three degrees of magnitude, primary ones between units within the chain, secondary ones between chains within the crystallites and tertiary or micellar ones between crystallites within the cellulose mass as a whole. (Fig. 6.)

The precise nature of secondary valence appears to be still an unsettled matter. Some are of the opinion that once the secondary valence bond is formed, it is indistinguishable from a primary one. If one always thinks of valence as a bond which can be represented by a line, then the forces which unite the cellulose chains into bundles, and also those which tie the bundles together to form a block of cellulose, are not true valences. One has, therefore, to resort to "association forces" of one kind or another. "Residual valences" are of this type. But forces such as those which tie cellulose chains into micellae must be recognized as stronger bonds than the association forces present in matter in general. This is true because molecular dispersion is apparently never reached when cellulose goes into "solution." Cellulose solutions and solutions of cellulose derivatives all contain aggregates (crystallites or micellae); in other words, all cellulose solutions are colloidal. The chains in a micella hold together more tightly than do the micellae, but not so firmly as do the glucose units of a chain.

Meyer and Mark estimate that the heat of separation of two cellulose chains would be one or two million calories, many times more than the heat of separation of a carbon-carbon bond (primary valence) which is 75,000 calories.

These speculations and hypotheses, uncertain as a number of them are, support the now generally held

view[15] that the structure of cellulose is represented by the formula $[(C_6H_{10}O_5)_x]_y$, where x equals the number of $C_6H_{10}O_5$ groups in the "molecular" chain, and y the number of $(C_6H_{10}O_5)_x$ groups joined by association, polymerization, or other forces to produce the micella or colloidal particle.

Sizes of cellulose micellae, as determined by X-ray measurements and diffusion experiments, are as follows (as given by Herzog); hemp fiber, 117 A.U. long (an Ångstrom unit is 10^{-8} cm, or 0.1 mμ[16]), and 66 A.U. in diameter: cellulose nitrate of hemp (solid state), 158 A.U. long: colloidal particles of nitrated hemp (dissolved) 74 A.U. in diameter. Averaging these values with those of Meyer and Mark, we find that the length of a micella, and therefore of the cellulose chain, is 100–200 A.U., with a diameter of the fascicle of about 50 A.U. We have given the length of an anhydrous cellobiose link as 10.3 A.U. A minimum of 20 of these units (the equivalent of 40 $C_6H_{10}O_5$ groups) gives about 200 A.U. as the length of the cellulose chain, the nearest approach to a cellulose molecule. Meyer gives 6 A.U. for the width and 3 A.U. for the thickness of the glucose unit. Hengstenberg and Mark[17] claim to have measured not only the size but the shape of these particles by X-ray methods. They found the crystallites in ramie to be about 600 Ångstrom units long and about 50 in diameter. This would alter the previous conclusions only in presenting evidence of still longer chains.

I have chosen cellulose for comparison with protoplasm simply because the chemists have found out more about it from the point of view of structure than about any other substance which is as closely related to protoplasm. I realize, however, that in doing this I am neglecting that substance or group of substances which I have repeatedly emphasized as representing the ultimate and funda-

[15] H. LeB. Gray and C. J. Staud, *Chem. Revs.*, 4: 355 (1927).

[16] mμ is the recognized correct symbol for the commonly used μμ.

[17] *Z. Kristallographie*, 69: 271 (1928).

mental material in protoplasm, namely, the proteins. But cellulose and protein are much alike in certain of their physical characteristics; further, the structural formula which the chemists have given us for cellulose is very similar to that which is believed by many to represent the type and arrangement of units in an elastic protein jelly such as gelatin.

Chemically, cellulose is less closely related to the proteins than it is physically, but there is a group of intermediate substances which, with cellulose at one end and the proteins at the other, constitute a progressive series. Of these intermediate substances several have been investigated by X-ray analysis and have been shown to be not only crystalline in nature but constituted of a structural framework similar to that which has been described for cellulose. The first of these substances is chitin, which gives a Röntgen diagram depicting a fiber period of 10.4 A.U., practically identical with that of cellulose, which is 10.3 A.U. (This value is the length of one link in the cellulose chain, the equivalent of two glucose residues or one anhydrous cellobiose molecule.) The micella of chitin is built up of some 1,000–2,000 acetyl-glycosamin residues.

Rubber is a rather special case. X-ray analysis reveals an amorphous ring in unstretched rubber but shows a crystalline spot pattern when the rubber is stretched, due to reorientation of structural units. The rubber micella is built up of isopren residues, or, more accurately, of the residues

$$-CH_2-CH=\underset{\displaystyle CH_3}{\overset{\displaystyle |}{C}}-CH_2- \quad \text{or} \quad -CH=CH-\underset{\displaystyle CH_3}{\overset{\displaystyle |}{CH}}-CH_2-$$

The construction is rhombic. The length of a micella and, therefore, the average length of a primary valence chain is 300–600 A.U., which represents 75–150 isopren residues. Meyer suggests that the elastic properties of rubber are due to the fact that the chains can be bent.

Clark[18] has shown by X-ray analysis that ordinary rubber crepe shows an "amorphous" diagram of two very broad diffuse rings. Upon stretching above 75 per cent., crystal fiber interferences appear which yield the dimensions of the unit cell, $8.1 \times 12.3 \times 8.3$ A.U., and the unit formula $(C_5H_8)_8$. Rubber of 10,000 per cent. elongation has been regarded as distinctly crystalline as any pure organic compound. Some prefer, however, to view this as a pseudo-crystalline state since the orientation is not permanent. It is interesting to note that Clark[19] regards the whole phenomenon as due to the hydrocarbon and not to proteins or impurities.

Natural silk (according to Herzog) shows a clear fiber diagram. The structural units are (according to Brill) glycyl-alanyl residues. Four of these build up an elementary unit.

Less clear is the crystalline structure of sinew and like matter. This is probably due to the fact that the crystallite is not composed of similar structural units, and is, therefore, of irregular structure.

There is every reason to believe that other highly polymerized substances of colloidal nature such as albumin, lignin, and reserve substances and therefore protoplasm itself, are constructed on the same principle of primary valence chains.

The work which I have here reviewed substantiates the hypothesis of Nägeli, that matter which forms gels and jellies is micellar in structure. On the contrary, there are those[20] who hold that the molecule is the structural unit of systems like gelatin, and that there is no intermediate unit such as a micella, except during gelatinization, *i.e.*, while the (gelatin) mass is cooling.

That which primarily interests us here is that regardless of the existence of any intermediate unit such as a

[18] *Nature*, 120: 119 (1927).

[19] *Ind. Eng. Chem.*, 21: 128 (1929).

[20] J. A. Wilson, "The Chemistry of Leather Manufacture," New York, 1923.

micella or other type of aggregate, the ultimate unit of structure is a chain molecule. When fascicles do exist, as in the case of cellulose, these two are linear.

In rereading the thoughtful discussion of Taylor[21] in his paper on the neuromotor apparatus of Euplotes, I was much interested to note that the fibrils of this protozoan are not highly elastic. Taylor states that the anal cirri fibers are frail, readily flexible and not resilient. They may be pulled in two by microdissection needles without showing any indication of stretching. He adds, they can, therefore, hardly function as contractile structures. I take it that they may be regarded as very efficient conductors. Now, for good conductance a parallel end-to-end orientation is the desired arrangement of fibrous units, while for elastic and resilient qualities a "brush-heap" distribution is preferable.

Disordered and ordered arrangements of micellae are given by Meyer[7] for substances of the cellulose group. In ramie (Fig. 7, A) the micellae lie in a regular, parallel

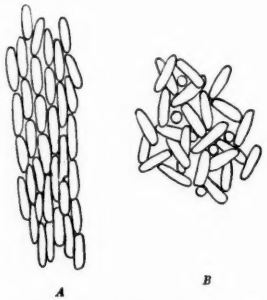

FIG. 7. *A*. Orderly, end-to-end arrangement of micellae in cellulose. *B*. Disordered, "brush-heap" arrangement of micellae in cellophan (after Meyer).

end-to-end order, while in cellophan (viscose rayon) the arrangement of the micellae is a haphazard one (Fig. 7, B); in the latter case we have what the chemists have characterized as a "brush-heap." How far the two

[21] Univ. Calif. Publ. Zool., 19: 403 (1920).

types of structure fit in with the physical properties of the substance is yet to be determined.

There is another important characteristic of the structural background of cellulose, proteins and protoplasm, which is an evident result of the type of structure here described. This characteristic is continuity. The mechanism of such processes as contractility and conductivity is not readily conceived except on the basis of continuity in structure. Continuity is now regarded as very typical of matter in general. It is believed to exist even in thermally agitated liquids.

Let us consider the simple case of water. The water molecule may be pictured in various schematic ways: as a triangle (Fig. 8, A); as a large oxygen atom with two

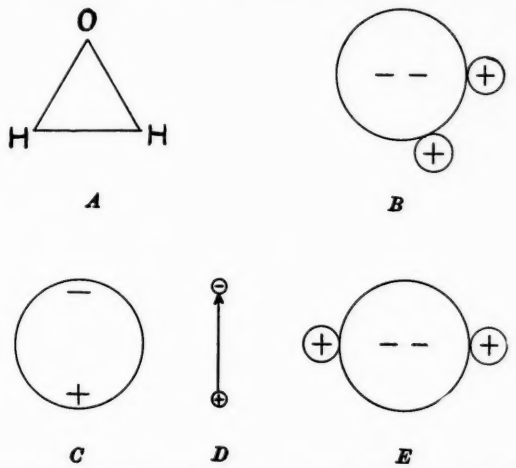

FIG. 8. Diagrammatic interpretations of the water molecule.

small hydrogen atoms attached to it (Fig. 8, B); as a simple dipole, schematized either as a molecule (Fig. 8, C) or as a symbolic arrow (Fig. 8, D), whose inner configuration we do not know with certainty but which yields a body one pole of which is positive and one negative; or our diagrammatic representation can be more in keeping with modern atomic theories and the two hydrogens

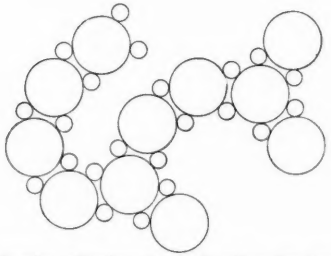

FIG. 9. Water molecules clinging to each other by loose residual electrostatic attraction to form a single huge molecular aggregate.

placed opposite each other, linked to the outer shell of the oxygen atom (Fig. 8, E). The justification of these frankly diagrammatic models lies in the recognized belief that the water molecule has an electric moment (polarity). In other words, the water molecule does have some of the characteristics called for in these models. It does act like two charges, one positive and the other negative, separated from each other, and the magnitude of the moment, that is to say, the product of the effective charge multiplied by the distance between this charge and its counterpart of opposite sign, is about 2×10^{-18} e.s.u.

With any of these models it is possible to build up a continuous framework. Thus, with the model shown in Fig. 8, B, the two positive hydrogens of one water molecule readily attach themselves to the oxygen atom of another at a point somewhat removed from the second molecule's own hydrogen pair (Fig. 9). Such weak intermolecular bonds are possible because the water molecule, though electrically neutral as a whole, becomes distinctly polar to a neighboring molecule which is in close proximity to it; that is, from a distance the molecule is neutral since the two negative charges of the oxygen atom and the positive charges of the two hydrogen atoms mutually neutralize each other, but either of these charges exercises a residual attraction for other molecules when in very close proximity to them.

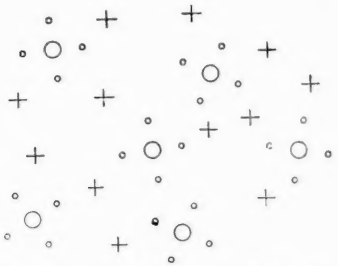

FIG. 10. Huggins' diagrammatical representation of water. Large circles denote oxygen kernels; crosses, hydrogen nuclei, and small circles, valence pairs.

The intermolecular linkage between water molecules is weak compared with the primary valence bonds of the hydrogen and oxygen atoms within the molecule. The adjustment which must be constantly going on in flowing water, or in a thermally agitated liquid, takes place at the point of intermolecular contact. Thus do we have continuity in structure in liquids without interference with known properties such as the capacity to flow. The firmer the intermolecular bond, the more nearly does the substance approach the solid state, but whether liquid or solid, a continuous framework exists. Viewed in this light the Atlantic Ocean becomes a single molecule.

Huggins[22] has drawn a somewhat similar picture (Fig. 10) of continuity in the structure of water, and contrasts such a non-molecular liquid (*i.e.*, one in which the polar molecule loses its identity when associated with others like itself) with a liquid of non-polar molecules like carbon tetrachloride which contains actual individual molecules of CCl_4. The latter liquid lacks the continuity in structure characteristic of water.

We can now consider in more detail the extent to which we are justified in applying to protoplasm these hypotheses on the structure of matter, in particular, of cellulose. What properties of protoplasm demand such a structure? Have structural features in protoplasm been

[22] *J. Chem. Ed.*, 3, Nos. 10, 11 and 12; Nos. 1 and 2 (1926–27).

seen which indicate that their ultimate unit is such a one as here described? Enough has already been said to indicate that the answer to both of these questions is, Yes.

Elasticity as an indicator of protoplasmic structure is the subject of a previous article already referred to. Glutinosity, swelling and coagulation are other typical characteristics of protoplasm which demand the linear unit. Of these let us consider swelling.

The firmness of a block of hydrated gelatin can exist only in virtue of a structural framework; further, that framework must be of a type which is capable of such readjustment as to permit a marked change in volume on the addition or loss of water without change in the amount of gelatin. This is impossible in a system built of spherical or like bodies, but readily accounted for on the basis of an adjustable framework of linear units. Nerve fibers are built up of linear units, "rod-shaped micellae," of ultra-microscopic dimensions. This has been shown to be true by Ettisch and Szegvari[23] for *N. ischiadicus* of the frog (from dark-field observations). These authors believe that the chemical and physical properties of connective tissue fibers are expressions of the characteristic form and orientation of their molecules.

The cytologist is familiar with many kinds of fibrous structures within cells. Calkins,[24] Minchin[25] and Taylor[21] have demonstrated the presence and function of special contractile and conductive fibers in ciliates such as Euplotes, Stentor, Spirostomum and Vorticella (both in the cell body and in the stalk). Since contractility and conductance are properties of all protoplasts, are exhibited to so marked a degree, albeit in a very elementary way, in white blood cells, and in simple unicellular organisms such as Amoeba and Vaginicola, may we not assume that though there exist no specialized fibrils in these most primitive states of organized living matter there must

[23] *Protoplasma,* 1: 214 (1926).

[24] "The Biology of the Protozoa," Philadelphia (1926).

[25] "Introduction to the Study of the Protozoa," London (1917).

yet be a relatively undifferentiated fibrous system in the protoplasm to account for the properties of contractility and conductance which in higher forms are primarily restricted to specialized structures?

Taylor[21] has expressed a similar point of view in saying that one general property of protoplasm is the propagation throughout all its substance of an excitation wave effected by a stimulus. To make this possible there must be a morphological continuity of the living substance. In the simplest organized bit of living matter specialized conductive structures are therefore unessential, but with increase in complexity there comes, first in the "unicellular" protozoan, localization of excitation stimuli in special organelles. These differentiated structures are derived, so Taylor[26] believes, through differentiation, condensation of molecular components out of the generalized state of protoplasm, back to which state they may go by dedifferentiation through resorption.

Relatively undifferentiated protoplasm often exhibits a fibrous structure in fixed cells such as that shown in the egg of Marsilia as drawn and described by Haberlandt[27] from material of Strasburger (Fig. 11). Figures of this kind have been regarded as artifacts, but artifacts arise only from preexisting conditions which determine them. The fibrous structure seen in fixed cells may be the result of coagulation at death but only of already existing strands or fibrous units of colloidal or molecular dimensions, the agglutination of which yields linear aggregates of microscopic size.

Scarth,[28] from observations on the Spirogyra chloroplast through polarizing prisms (crossed nicols), concludes that protoplasm is like a liquid crystal. He states that when a chloroplast is made more fluid by reagents and then again regelatinizes, the double refraction returns with even greater brilliancy, showing that the

[26] *Physiol. Zool.*, 1: 1 (1928).
[27] *Sitzungsber. d. preus. Akad. d. Wiss.*, 2: 4 (1922).
[28] *Quart. Jour. Exp. Physiol.*, 14: 99 (1924).

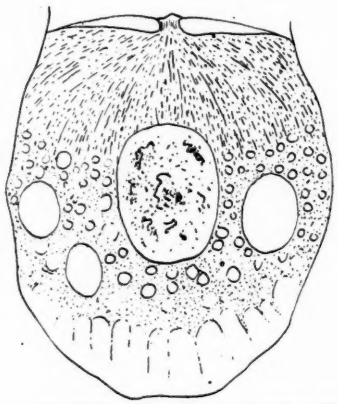

FIG. 11. The egg cell of Marsilia (fixed) showing fibrous nature of the cytoplasm. (After Haberlandt from material of Strasburger: published with the kind permission of Professor Haberlandt.)

molecules or crystalline particles again orientate along definite axes.

The most encouraging feature of the problem of the structure of non-living and living matter is that a general type of structure appears to distinguish all systems which have certain physical properties in common. High conductivity means parallel arrangement of linear particles whether we have to do with copper or nerves. The contractile qualities of such jellies as cellulose, rubber, gelatin and protoplasm are attributable in each case to a long and tenuous structural unit.

SHAKER, A NEW MUTATION OF THE HOUSE MOUSE (*MUS MUSCULUS*)

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IN a stock of normal albino mice, known as the Bagg albino strain, there appeared in two families individuals showing distinctive behavioristic characters. This strain was in the colony of Dr. E. C. MacDowell, and had been pedigreed and inbred by him for twelve to thirteen generations.

In the twelfth generation of one family there appeared, among the progeny of each of four litter-mate females mated to a litter-mate male, individuals showing this mutation. In the thirteenth generation of the other family, the same mutation appeared among the young of two litter-mate females bred to their sib. These two families had a common origin in the tenth generation of inbreeding, so it is probable that the mutation occurred but once, but remained latent due to matings with homozygous normals till the twelfth and thirteenth generations, respectively.

For the sake of simplicity, the term "shaker" and the symbol "sh" have been adopted to indicate this mutation.

DESCRIPTION

The mutation shows itself principally in the form of "nervous head movements": rapid, successive jerkings of the head upward, accompanied by sniffing and twitching of the vibrissae. However, the shaker can, for short intervals at least, cease from the head shakings and appear perfectly normal, as when the animal is eating, drinking, in defensive attitudes, or when first presented with a new situation, such as the removal of the pen cover, or upon being placed on the floor.

The animals sometimes run in circles, but hardly as intensely or in such small circles as the Japanese waltzing

mouse, and seldom, if ever, spin with one foot pivoted. The circling behavior, while probably dependent to some degree at least on the particular state of nervousness, seems to be characteristic of some individuals only. Out of 114 shakers tested, sixteen, or 14 per cent. were classed as circlers; of these, five were males and eleven females. Among all circlers, both male and female, there is a marked tendency to circle counter-clockwise. Of the sixteen circlers but four circled clockwise, the other twelve counter-clockwise. No left-turning circler has been observed to circle clockwise. In this respect again the shaker differs from the waltzer, in which exclusive circling to one side is rare. The number of continuous circles the shaker will make is also limited as compared to the waltzer; the former will rarely exceed thirty turns, while the latter will frequently circle or whirl a hundred times or more without stopping. The shaker will rarely entangle its feet in loose cotton, while the waltzer will do so frequently. The Japanese waltzer's characteristic of circling around an object is not common in the shaker. Of the circlers tested above, only four were recorded as circling around objects.

Released on a cold concrete floor, the shaker appears at a complete loss as to what to do. It will not attempt to run away; frequently it will sit perfectly still, head down. When allowed to stay on the floor for a period of ten minutes, the shaker will seldom travel more than a total of six feet, and this distance is covered in short, jerky starts and stops. The circlers appear to be somewhat more active on the floor than non-circlers. The tendency to circle is sometimes more marked on an unfamiliar surface, such as a table, floor, etc. The shaker can, and at times does, travel in a straight line for almost any distance, particularly if the situation and surface are familiar.

The reaction to being suspended by the tail is usually characteristic, but varies in degree. In the extreme, it is represented by tetanic contractions of the voluntary muscles; trunk and limbs quite rigid and quivering,

ears bent forward, eyes partly closed, mouth open and fur bristling. Upon being released the mouse will usually recover at once, or the catalepsis may be broken by a tap on the head or body.

The animals are highly active and nervous, and when excited run wildly in circles or haphazardly, showing lack of coordination of nervous control. The entire condition seems to be associated with the central nervous system, and might be classed as a type of chorea.

The choreic condition is sometimes noticeable at birth and commonly a few days later. When placed on a flat surface, the animals will throw the head backward, or twist the anterior part of the body to one side. At this age their actions are quite similar to that of young waltzers. At twelve to fourteen days of age the behavioristic character is usually clearly developed, and by three weeks is quite typical. Rarely, the characteristic head movements may not show in the fully developed form till the animal is three or four weeks old. With age the shaker becomes somewhat phlegmatic and is neither as nervous nor as active as when younger. It will even add weight in the form of fat.

Adult shakers, so far as they have been tested, show no reaction to sound. Sixty-two mature individuals, varying in age from two months to one year, have been carefully tested and all are apparently completely deaf. The deafness, however, does not seem to be a congenital defect, but comes on at an age varying from twenty-two to thirty days. Young shakers show typical reaction to sound, fully equal to that of the normal mouse. This reaction is evident from the time the ears open, up to an age of three or four weeks. Two young shakers proved to be deaf at twenty-two days, while the oldest that gave positive evidence of hearing was twenty-nine days old. This last mouse was tested two days later and gave no reaction to sound. Thus the transition from the hearing to the deaf condition occurs more or less rapidly, within a few days at most, but varying in different in-

dividuals as to the age of incidence. There seems to be, therefore, a close correlation between the deafness and the full development of the character.

Individuals heterozygous for the shaker factor alone are normal in all of their reactions to sound, at least up to an age of more than one year.

For testing sound reactions a sharp, metallic click, made by snapping a pair of forceps together, was used. The authors find this the most satisfactory type of sound, on account of its sharpness, its minimum volume, freedom from accessory vibrations and the distinctive response it calls forth. It can be repeated almost indefinitely, and yet each time the ears or ear, if hearing is restricted to one side, will give a slight twitch.

On account of their nervous, active condition, shakers do not as readily accumulate fat, and are, therefore, under weight as compared to normal individuals of the same age. Food and moisture consumption are noticeably greater, as would be expected in such highly active animals. They appear to sleep soundly, and are not as easily awakened as normal mice.

Shaker females breed normally and are good mothers, there being no noticeable difference either with respect to breeding capacity, size of litter or the ability to raise young, between them and the average of the colony. Individual females have produced first litters at sixty and sixty-three days of age. The males, however, show a tendency towards sterility, which may or may not be overcome as the animal grows older. This, however, may be a functional sterility due to inability to mate on account of their lack of nervous coordination.

INHERITANCE

The shaker character behaves as a simple Mendelian recessive, and is probably due to a single factor or gene.

The parents of the original shakers, six females and two males, were indistinguishable from the rest of the strain, which, now in the sixteenth and seventeenth gen-

eration of inbreeding, has produced no shakers. But they must have been heterozygous for the character, as their progeny consisted of seventy normals and twenty-seven shakers, a fair enough approximation to the theoretical ratio, 3:1, of a recessive. To these numbers may be added the young from heterozygous individuals of later generations. The total number of offspring from all such matings is 142, of which 103 were normal and 39 shakers. The expectation on a 3:1 basis of a population of this size would be 106.5:35.5. The difference, 3.5, with a probable error of $\pm$ 3.4, is not significant.

Shaker females backcrossed to the original heterozygous male produced forty normals and thirty-seven shakers. Other backcross matings of heterozygous individuals to shakers have produced thirty-five normals and thirty-four shakers. Thus we have a total population produced by a backcross of 146, seventy-five normals and seventy-one shakers. Mendelian expectation of the progeny of a backcross is a 1:1 ratio. The actually observed ratio is thus strikingly close to expectation, the difference being so small that it can indicate nothing but random sampling.

Shaker mice, bred to shakers, breed true; they have produced to date 103 young, all shakers, showing the recessive nature of the character. Outcrossed to normal, the character can be recovered in the F_2 without any loss in expression, and can then be inbred true to type in succeeding generations, thus indicating that the mutation is due to a definite Mendelizing gene or factor.

Homozygous normal individuals mated to shakers have produced to date sixty-seven young, all normal. Homozygous normal females backcrossed to one of the original heterozygous males have produced nine young, all normal; such females mated to other heterozygous males have produced fifteen young, all normal. These numbers are sufficient to indicate a dominance of the normal character, complete as far as can be observed.

Inasmuch as this character, shaker, resembles in some respects the character found in the Japanese waltzing mouse, it was thought that it might be another expression of the nervous deficiency of the waltzing factor. A cross was, therefore, made between shaker females and an extracted waltzer male. This mating produced thirty-two males and thirty-one females, all perfectly normal in behavior, gait and hearing. A second cross, between shaker females and a pure Japanese waltzer male, has yielded to date thirty-six young, fourteen males and twenty-two females, all normal. We conclude, therefore, that the shaker character is due to a gene distinct and different from that of waltzing.

The above results also indicate that the shaker factor is not sex linked; if it were, from the nature of the cross all males would be shakers, because the sex-chromosome mechanism of both the house mouse and the Japanese waltzer is of the x y type, with males heterozygous. To these crosses may be added the young from three additional litters, the progeny of shaker females bred to related homozygous normal males, four males and eleven females, giving a total of fifty males and sixty-four females, all normal. The absence of shaker males among the young of shaker females bred to non-shakers proves that the factor shaker is not carried in the sex chromosome.

The F_1 individuals heterozygous for the two factors, shaker and waltzing, both of which produce deafness in the homozygous state, although perfectly normal as to hearing ability when young, have a tendency to become deaf at an age of three or four months and older. Out of fifteen such double heterozygotes three months old, six gave no reaction to sound, while the remaining nine gave some reaction; only one, however, seemed to be normal. Of twenty-two individuals six months or more of age, only four gave any evidence of hearing, and none of these equal to the normal. This condition is interesting in connection with the statement made above that individ-

uals heterozygous for the shaker factor possess normal hearing for at least one year; older animals than this have not been tested. The F_1 individuals heterozygous for the waltzing gene are likewise normal with respect to hearing throughout their lives. Numbers of such individuals have been tested which were over two years old (Gates 1926). The combined heterozygosity of each factor, therefore, seems to exert a cumulative effect on the sense of hearing, tending to produce deafness at full maturity.

Discussion

Hereditary nervous disturbances are known in both man and animals. Circus movements, reported in mice (Fortuyn, 1912, and others), in rats (Bonhote, 1912), in rabbits (Cole, 1922), congenital palsy in guinea pigs (Cole and Ibsen, 1920), ataxia of pigeons (Riddle, 1918) and the behavior of parlor tumbler pigeons appear due to aberrant nervous conditions.

The shaker characteristic partially resembles some of the types of chorea found in man and animals. Huntington's chorea with its uncontrolled muscular jerkings might be considered as the most similar. However, in the shaker there is at times perfect control; and moreover Huntington's chorea behaves as a Mendelian dominant, while the shaker characteristic is recessive. Other types of chorea appear to behave as recessives, but here again we find a difference in the ability in the one case and the inability in the other to control the voluntary muscles.

Miss Dorothy Loomis has recently sent the junior author a few individuals from her stock of circlers. These are interesting in that the animals themselves are quite phlegmatic, are stimulated with difficulty, and yet some individuals are prone to circling.

Circling has also appeared in an entirely different strain in the MacDowell colony. Among 1,600 mice raised in this strain within three years, fifty-seven circlers, 3.5 per cent., have been observed. Three main differences appear between these and the shakers: no

nervous head movements have ever been observed; they have perfect hearing; and they show this habit only after maturity, the age of incidence varying from fourteen weeks to one year. Individual circlers are often closely related. Test matings in considerable numbers have been made, but as yet the condition of the offspring can not be predicted. The facts that this type of circling is confined to this stock, that it is found more frequently in certain families and that its appearance still remains sporadic, point to a definite inheritance, but due probably to several or many genes.

Linkage relationships of the character shaker to other mutations of the house mouse are being investigated.

SUMMARY

This report describes a new behavioristic mutation, shaker, of the house mouse, which expresses itself in the form of nervous head movements, circling and deafness, and which behaves in inheritance as a single gene character, recessive to the normal and not sex linked. It differs somewhat in its expression from waltzing, and is shown to be due to a different factor or gene from that of waltzing.

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THE NATURAL HISTORY OF CLADOCERANS IN RELATION TO TEMPERATURE—III. PRE-ADAPTATION AND DISPERSAL

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THE extent of dispersal of animals depends upon an equilibrium between those factors which aid and those which hinder such dispersal. The aids to the dispersal of animals are generally classified into two groups. The first of these includes the locomotion of the animals themselves from place to place by swimming, walking, etc.; the second is passive transportation. The latter means of dispersal may be accomplished by currents of wind or water, floating debris or directly by other animals. Both Darwin and Wallace recognized and extensively dealt with the devious ways by which animals might be carried to more distant regions. That animals are so carried by fortuitous means is well substantiated by the many reports of animals that have been found hundreds of miles from their normal habitat. Small aquatic animals, such as cladocerans, have at least two possible means of becoming widely distributed. The animals themselves being feeble swimmers may be carried by rivers and streams from one pond or lake to another in time of flood; the ephippial eggs, which can withstand desiccation, may be carried by floating vegetation or by the more classical method of being transported in the mud adhering to the feet and legs of water birds. It can not be doubted that the winter eggs and perhaps the animals have had every opportunity to establish themselves in every region of the earth; this view is supported by the fact that a great many of the species are so generally distributed. *Chydorus sphaericus* is reported from all parts of the world. The wide distribution of the genera *Daphnia, Moina* and *Simocephalus* has already been

referred to (Brown, 1929a). The wide distribution of *Pseudosida bidentata* in all tropical regions is another example that may be mentioned (Birge, 1910). Sometimes the majority of the species of a large group of animals like the Protozoa may be practically universal in occurrence. The problem, then, is not to explain the *presence* of a species in any region, but rather the peculiar *absence* of certain species from localities where they might be expected to occur.

The barriers to the dispersal of animals may be divided into organic and inorganic. The former consist chiefly of competing species of animals. In the case of Cladocera the chief enemies are fish, fresh-water hydra, some types of insect larvae and certain carnivorous water plants like *Utricularia*. Such enemies are not local but are widely distributed and can not be held accountable for the non-occurrence of daphnids over a large territory. The inorganic barriers for fresh-water animals consist of such agencies as large areas of land, the salinity of the sea and temperature. The first two of these can be overcome by the peculiar method of dispersal of Cladocera, but the temperature of the water into which the animals are accidentally deposited may be the deciding factor in their perpetuation.

Many writers have given accounts of the manner in which extremes of temperature act to restrict the occurrence of animals. A few typical cases of such restriction selected from a large number of available instances may be mentioned. Tower (1906) speaks of the low temperature of the north and the high temperature of the south as having established seemingly effective barriers to prevent the potato beetle from extending its present limits. Mayer (1914) finds that there is a close correlation between the resistance of corals to high temperatures in the laboratory and their habitat temperature. He found, for example, that corals of the shallow-reef flats, where the temperature range is greatest, are the most resistant to both heat and cold, while those of deeper water are the

least resistant; other forms living in shallow but freely circulating water show moderate powers of resistance. He also subjected the coral animals to a low temperature such as would correspond to that produced by the coldest "norther" of winter. He concludes from such tests that certain species would survive a prolonged "norther" without injury, other species would be injured but survive, while to certain species this temperature (13.9°) would prove fatal. Marsh (1918) thinks that the temperature is the one great controlling factor in the distribution of copepods; he illustrates this by three species of the same genus:

> *Diaptomus minutus* is found from Greenland and Iceland south to the northern tier of states in the United States, but does not occur south of 42° to 43° N. L., *Diaptomus sicilis* is confined to the northern tier of states. *Diaptomus siciloides* is found in a band farther to the south, being limited roughly to the region between the thirty-sixth and forty-third parallels. These three species are closely related to each other in structure, and presumably are of the same line of descent.

Many other similar cases are mentioned by Marsh. Parker (1919) believes that the scarcity of the sea anemone *Sagartia luciae* at Woods Hole, Massachusetts, during the summer of 1918 was directly traceable to the preceding severe winter. That this effect was due to the low temperatures and not to the mechanical action of ice was indicated by the presence of other sea anemones which have a more northerly range. Allee (1923) also found that the winter of 1918–19 caused but 18 per cent. of all north-ranging species in the vicinity of Woods Hole to be noticeably fewer in numbers the following summer, while 48 per cent. of the south-ranging species were similarly affected. He concludes, "The southern extension of north-ranging species is limited by the high summer temperatures of the flats, just as in shallow water the extreme winter cold limits the northward extension of south-ranging species."

Experiments with many species of Cladocera (Brown, 1929a) have shown that certain species, such as *Moina macrocopa* and *Pseudosida bidentata,* are unable to with-

stand cooling to 0°, while other species live and reproduce at this temperature. And, conversely, the two species just mentioned live and reproduce at a temperature which is high enough to be lethal for other species, such as those of *Daphnia, Simocephalus, Sida,* etc. While *P. bidentata* is a southern form and is probably restricted to such latitudes by its inability to endure low temperatures, *M. macrocopa* is a summer form and for an analogous reason does not occur during the winter in northern regions. *D. pulex, D. longispina* and the species of *Simocephalus* have a moderate resistance to higher temperatures and are not killed by low temperatures. These species are widespread, occur during the winter, but are scarce in the summer. *Sida crystallina,* which shows a very low resistance to higher temperatures, is not only restricted to the north but also to the cooler months of the year. It must be kept in mind that the ephippial eggs can withstand freezing and desiccation, and that a species is represented by these eggs during months of the year when environmental conditions are adverse to parthenogenetic reproduction.

The periodic appearance of sexual females and males, which usually comes at the close of a period of maximum numbers of individuals, has been considered by many writers as due solely to some inherent sexual cycle proper to the species (Weismann, 1876–79; Keilhack, 1906; Kuttner, 1909). Others (Issakowitsch, 1908; Woltereck, 1909; McClendon, 1910; Papanicolau, 1910; Grosvenor and Smith, 1913; Scharfenberg, 1914) have held that there is an innate sexual cycle, but that it is to some extent modifiable by the environment. Banta (1913, 1914, 1915, 1925a) and Agar (1914) have shown conclusively that this apparently cyclic character of the appearance of males and sexual females is due solely to environmental causes. Grosvenor and Smith (1913), Banta and Brown (1923) and Banta (1925a) have shown that at least the appearance of males is associated with the crowding of the

females and is also dependent to some extent on the temperature (Banta and Brown, 1925b).

While the presence or absence of cladocerans in a given locality during certain months of the year is controlled by the extremes of temperature, the relative density of population of species whose temperature ranges overlap is determined by the speed of the generation cycle and the frequency of brood succession; that is, upon the extent to which a rising temperature accelerates development or a lowering temperature retards development. Some species, like *M. macrocopa* and *P. bidentata,* as determined by the magnitude of their temperature coefficients for development (Brown, 1929b), develop with greater acceleration for each five degree rise in temperature than do the species of *Daphnia* and *Simocephalus.* Such differences may be measured also by examining the magnitude of the temperature characteristics (Brown, 1926–27) for development and the location of critical temperatures above which the acceleration in development with rise of temperature is less. This is very well shown by an analysis of data on beetle larvae given by Blunk (Brown, 1929b). For one species, *Dytiscus marginalis,* a slower rate of development did not supervene until 15°, while for the other, *D. semisulcatus,* this occurred at 10°. The former species has its maximum of abundance in the summer and the latter sometime during the winter. A similar agreement between the values of the temperature characteristics and critical temperatures in relation to brood succession was seen in *M. macrocopa* and *S. serrulatus.* In this instance *M. macrocopa,* the summer form, is enabled to "take advantage of" a rising temperature by producing broods in quicker succession than the winter form *S. serrulatus.*

It is an interesting fact that frequently representatives of many species of cladocerans may be found at a given time, while again the same location or similar pond nearby may be populated with thousands of individuals of only one or two species. When maximum numbers of a single

species are present, other forms seem to be absent. The number of individuals seems to be inversely proportional to the number of different species present. Or, among the small crustaceans that have similar habitats, a collector often finds moderate numbers of copepods, ostracods and cladocerans at the same time, but when one of these groups is present in enormous numbers the others seem strikingly scarce; this is also particularly true of the complementary occurrence in small ponds of daphnids and ostracods, for example, *Moina* and *Cypris* (observed in a small pond near Cold Spring Harbor, Long Island). If the conditions of food, temperature and the like are especially suitable for the rapid multiplication of a particular species, then this form will show the greatest number of individuals, while if the environmental conditions are not so specifically suitable many species may be present in fewer numbers. As Crozier (1923) has pointed out in relation to the fauna of a sewage filter "film," this connection between the numbers of individuals and the diversity of kinds of organisms represented may be a means of estimating the comparative "selective stringency" of environments.

The method whereby animals invade new territory has been the subject of much discussion and some experimentation. Dallinger (1887) found that if a colony of flagellates, the individuals of which normally are killed at 23°, was gradually (during several years) subjected to higher and higher temperatures it could ultimately be maintained reproductively active at 70°. Davenport and Castle (1896) found that the temperature necessary to cause tadpoles to go into heat rigor could be raised about 3° by keeping the animals at 24.5° for four weeks instead of at the usual temperature of 15°. Vernon (1889) found that the lethal temperatures of certain marine invertebrates collected in the summer were slightly higher than for the same species collected in the spring. These observations on acclimatization of animals to higher tempera-

tures and the wide distribution of many species of animals have led many writers to conclude that organisms readily adapt themselves to new ranges of temperature. This view is strengthened by the long and diverse lists of animals and plants that may occur in hot springs (Hoppe-Seyler, 1875; Plateau, 1872; Brues, 1924) and in deserts (Buxton, 1924). Some animals show remarkable powers of becoming adjusted to higher or lower temperatures over comparatively short ranges of time as Loeb and Wasteneys (1912) have shown for *Fundulus* in the case of higher temperatures and Ackerman (1926) for grain aphids for lower temperatures. Jennings (1920) thinks many of the slightly varying stocks found among protozoans may owe their origin partly to the inherited effects of long continued environmental diversities. Jollos (1913, 1914) finds that protozoans respond readily to increasing temperatures by showing higher lethal temperatures and that possibly in one case this change persisted after conjugation; Middleton (1918) finds certain differences in fission rate of *Stylonychia* following prolonged exposure at higher and lower temperatures, but these strains when returned to an intermediate temperature show fission rates that are contradictory in different series of experiments. Jacobs (1914), on the other hand, finds that certain parasitic ciliate protozoans, after presumably having been in the same environment for a very long time, still possess characteristics which are physiologically distinct. And Northrup (1919–20) failed to find any evidence of hereditary adaptation to higher temperatures in *Drosophila.*

The actual changes in the protoplasm of animals when acclimatized to higher temperatures has been variously considered as loss of water from the tissues (Davenport and Castle, 1896; Vernon, 1899; Brues, 1924; and others) and by others as due merely to increased viscosity of protoplasm at the higher temperatures. Bělehrádek (1926a) thinks protoplasmic viscosity is connected with the thermal adaptation of a given species. Loeb (1916)

suggests that the increase in temperature may bring about an increase in the permeability of the cells, or that substances might be formed in the body at higher temperatures which do not exist at lower temperatures. Disregarding such changes in protoplasm, if adaptation of animals to changes in temperature were the rule it would be difficult to see why cladocerans and various marine animals (*vide* Mayer) have not spread to all regions. Some daphnids, *i.e., D. pulex,* have apparently become very widely distributed, and yet this species is restricted to the spring and fall months. It is possible of course that the annual rhythm of a species may depend on food, or light or on other factors; but the relation to temperature is the obvious one.

Although many animals are widely distributed, this distribution may not be due to adaptation, for if adaptation were general then it is even more difficult to explain the absence of forms in regions adjoining those in which they are found. It is perhaps a better assumption to follow Cuénot (1911, 1923) and to speak of *preadaptation.* This idea was first formulated by Davenport (1903) in relation to the animal types found in a restricted habitat like the sand spit at Cold Spring Harbor; Loeb (1915, 1916) accepted this viewpoint and indicated how it might apply in relation to cave-animals. Loeb (1916) found that the heterogeneous hybridization of species of *Fundulus* produced blind forms, and he considers all blind animals (in caves and outside) as being mutations or due to some factorial changes in the germ-plasm of the animals. While "adaptation" then, as ordinarily employed, connotes some functional accommodation of the individual or species to a new environment, "preadaptation" implies that modifications by environment or by factorial recombinations exist *before* the animal enters into a new region.

In daphnids these preadaptations may be of several kinds genetically. It is known (Banta, Snyder, and Wood, 1926) that mutations appearing within a clone may

be passed on from one parthenogenetic generation to the next and even segregate as Mendelian characters in sexual reproduction. Banta (1925b) and Schrader (1925) have shown that the clone of *D. pulex* which has been designated as "Line 984," and which shows a marked difference from the typical *D. pulex* in its lethal temperature, is probably a hexaploid form and without males, the ephippial (pseudo-sexual) eggs developing parthenogenetically. More recently Wood and Banta (1926) report the interesting case of a clone of *D. longispina* which was started from an ephippial egg resulting from a controlled sexual cross within normal stock. This new clone has a temperature range that is markedly different from the parent stock. While the parent stock survives well at 20° and with difficulty at 27°, the derived clone is unable to continue itself at 20° but thrives at 27°. Such an animal, arising as the result of the recombination of genetic factors or through mutation, would be able to perpetuate itself in a region quite different in temperature from the habitat of the parent race. As this clone arose from a winter egg, and these eggs are easily transported to new regions, a possible method is apparent to account for the presence of animals of the same species living in widely different habitats. The distribution and occurrence of cladoceran species can thus be explained as due to the spontaneous appearance of genetically different individuals which are fortuitously transplanted to new and favorable environments.

Summary

Preadaptation is suggested as the best method of accounting for the existing distribution of the Cladocera; this method involves a change in the organization of the body relative to its resistance to extremes of temperature. Several of the types of genetical changes which may occur in these animals are discussed in relation to preadaptation to new temperature ranges.

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THE SPIDER FAUNA OF PANAMA AND ITS CENTRAL AMERICAN AFFILIATION

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VARIOUS theories have been advanced to account for the relationship between the spider fauna of the New World and that of the eastern hemisphere. One of these theories postulates a gradual dispersal through the Arctic with subsequent migration southward. Another points to a land connection between Africa and America in the form of the sunken "Atlantis," the migration of spiders along this connection and subsequent dispersal northward and southward after its disappearance. These theories are based on evidence derived from the study of the distribution of genera of both extinct and recent animals. But, whatever the origin of the American spider fauna in the distant past may have been, the study of the present fauna does not shed any new light on the problem. The number of species common to both hemispheres is not definitely known and is, moreover, represented to a considerable extent by cosmopolitan, cosmotropical and cosmoboreal species. The relative increase in Palearctic species as we proceed northward of the United States is very deceptive and coincident with a progressive decrease in the total number of species. And the knowledge of the Neotropical spider fauna is still lamentably inadequate, as is also that of tropical Africa.

Until recently it was, therefore, more or less natural to assume that the spider fauna of the American continent represents, as it were, a unit showing a gradual change from a tropical to a subtropical, temperate and finally boreal and austral character. This view found substantiation in the fact that there is no region on the entire continent, or even on the adjoining islands, where the existing fauna would not show an admixture of spe-

cies found in the adjoining regions. The somewhat sharper distinction between the South American and Central American spider fauna was easily explainable on the assumption that no extensive collections were extant from Costa Rica and Panama. My study of the Arachnida of Panama, published in 1925, has not only made this explanation untenable, but has also clearly demonstrated that the Central American fauna is quite distinct from the South American one and that the transition from the one to the other is rather abrupt. An analysis of the data available at that time has shown that fully 80.2 per cent. of species found in Panama do not occur in South America, that out of 369 species recorded from Panama only fourteen are also found in South America, while fifty-nine are either cosmopolitan or cosmotropical or neotropical, and that of the 296 species constituting the 80.2 per cent. of the total, 142 are indigenous in Panama and 154 are found only in Central America and Panama. Thus it became probable that at a less remote geological period than the paleozoic, there must have existed three distinct centers of evolutionary activity responsible for the appearance of numerous new species without any possibility or with but exceedingly limited possibility of migration from one center to another. This view, to which I give expression here for the first time, finds substantiation in the fact that Central America was separated at one time by a sea from both North and South America. According to Schuchert,[1] "probably during the late Miocene, but certainly in the early Pliocene, the Gulf of Mexico for the first time communicated freely with the Pacific Ocean through the Tehuantepec portal." And according to the same authority, "There was no Costa Rica and Panama apparently before late Cretaceous time." It will be remembered that the Tertiary spiders of both Europe and North America are already not only rich in species, but also closely related to the recent spiders of the cor-

[1] *Science*, 69: 144.

responding geographical regions. The Baltic amber, from which so many beautiful specimens and so numerous species have been described, is usually placed in the Lower Oligocene, while the Florissant spiders of Colorado are now referred to the Upper Miocene, or to that geological period when Central America was separated from North America by a sea.

The importance of the fact that the Central American spider fauna is distinct from the South American one will be still more appreciated when the geographical distribution of spiders in the Antilles becomes better known and understood. Being still in the midst of my researches on this subject I plan to give a detailed analysis of the Antillean fauna at the completion of my work on the spiders of Porto Rico, of which only the first part has been published in 1929. Nevertheless, the results at the time of publication were already sufficiently clear to permit the formulation of a theory of the distribution of spiders in the Antilles, published in *Science* in the shape of a brief preliminary statement. There appear to exist two distinct faunas, that of the Greater Antilles, having its origin in land migration from Central America, and that of the Lesser Antilles, showing relationship to Venezuela and having its origin in a dispersal through hurricanes. The reader will appreciate the feeling of grave concern with which I regarded the publication in February, 1929, by Nathan Banks of his paper on the "Spiders of Panama," in the introduction to which he unequivocally maintains the affinity of the fauna of Panama to that of South America. Banks lists 244 species collected on the island of Barro Colorado in the Gatun Lake, in the vicinity of Panama City and along the Panama railroad. Four of these species Banks was unable to identify beyond the genus, thus leaving 240 species for the entire region or 168 for Barro Colorado alone, since all four species mentioned come from that island and are included by Banks in his introduction in

the 172 species recorded.[2] One hundred and six species have been listed already in my paper as occurring in Panama and 134 species appear for the first time. Banks does not give any analysis of the fauna on the basis of his collections. With few exceptions, in listing the species he does not even mention the localities from which they were originally described or later recorded. Disposing of my conclusion in a few short sentences he expects the reader to believe his own statement because his collections were made "in the low land of the country," while mine came "from higher regions of Panama" —an assertion in itself not entirely correct—and because "a number of South American species were found here which were unknown or rare in Central America." This kind of interpretation of the affiliations of a fauna does not lead us anywhere and is, moreover, objectionable because, as we shall presently see, it tries to impress its correctness on the mind of the reader without giving any proof in its own support. To find out for myself the truth of the matter I have therefore undertaken the tedious task of subjecting Banks's paper to a careful analysis, using my own catalogue and more recent published data for information about the localities from which previously described species have been recorded. As in my paper on the Arachnida of Panama I divide the species into five groups each represented by its own column in the table. In the first column are listed for each family the number of species recorded only from Panama. For the present they must be considered as being indigenous. In the second column—only from Panama and Central America. In the third column—only from Panama and South America. In the fourth column all cosmopolitan, cosmotropical and neotropical species. The latter include all species recorded from Panama and countries north and south of Panama, regardless of whether they are more common in Central or in South America, partly because the existing records

[2] *Bull.* Mus. Comp. Zool., Harvard, 69: 54, 1929.

TABLE I—SHOWING THE GEOGRAPHICAL DISTRIBUTION OF SPIDERS RECORDED BY BANKS FROM THE LOWER REGIONS OF PANAMA

Family	Only from Panama	Panama and Central America	Panama and South America	Cosmopolitan Cosmotropical Neotropical	Total
Theraphosidae	(1)	0	0	0	1
Barychelidae	0	0	0	0	0
Dipluridae	0	0	0	(1)	1
Ctenizidae	0	1	0	0	1
Uloboridae	0	4	1	0	5
Acanthoctenidae	0	0	0	1	1
Zoropsidae	0	0	0	0	0
Dictynidae	0	0	0	0	0
Filistatidae	0	0	0	(1)	1
Sicariidae	0	(1)	1	(2)	4
Oonopidae	0	1	0	0	1
Caponiidae	0	0	1	0	1
Drassidae	2	0	0	0	2
Hersiliidae	0	(1)	0	0	1
Pholcidae	2	2	0	0	4
Theridiidae	4 (1)	5 (1)	7 (1)	5 (5)	29
Linyphiidae	1	(1)	1 (1)	0	4
Argiopidae	6 (2)	13 (17)	3	8 (14)	63
Mimetidae	0	1	1	0	2
Thomisidae	2 (1)	1 (1)	2	1 (2)	10
Selenopidae	0	1 (1)	0	0	2
Sparassidae	3	(1)	0	0	4
Clubionidae	5 (4)	4 (3)	1	0	17
Ctenidae	0	1 (3)	1	0	5
Agelenidae	0	0	0	0	0
Pisauridae	(3)	0	2	1 (1)	7
Lycosidae	2 (2)	(1)	0	0	5
Senoculidae	0	0	0	0	0
Attidae	13 (13)	15 (15)	1	2 (2)	61
Oxyopidae	(2)	1	1	(1)	5
Dysderidae	0	1	0	0	1
Zodariidae	1	0	0	0	1
Palpimanidae	1	0	0	0	1
Total	42 (29)	51 (45)	23 (2)	18 (29)	240
Per cent.	29.58	40.00	10.83	19.59	100

are not sufficient to indicate the frequency of occurrence, partly because species more common in South America are fully counterbalanced by others more common in Central America. The fifth column gives the total number of species. The figures without parentheses represent species for the first time recorded by Banks; those in parentheses, species already recorded for Panama in

TABLE II—GEOGRAPHICAL DISTRIBUTION OF SPIDERS RECORDED FROM PANAMA UP TO THE PRESENT DATE

Family	Only from Panama	Panama and Central America	Panama and South America	Cosmopolitan Cosmotropical Neotropical	Total
Theraphosidae	8	2	1	1	12
Barychelidae	1	0	0	0	1
Dipluridae	0	1	0	1	2
Ctenizidae	2	1	0	0	3
Uloboridae	0	5	1	1	7
Acanthoctenidae	1	0	0	1	2
Zoropsidae	0	1	0	0	1
Dictynidae	0	1	0	0	1
Filistatidae	0	0	0	1	1
Sicariidae	0	1	1	3	5
Oonopidae	1	1	0	0	2
Caponiidae	1	0	1	0	2
Drassidae	2	0	0	0	2
Hersiliidae	0	1	0	0	1
Pholcidae	2	4	0	3	9
Theridiidae	12	12	8	16	48
Linyphiidae	4	1	2	0	7
Argiopidae	21	68	4	33	126
Mimetidae	4	3	1	0	8
Thomisidae	14	11	3	4	32
Selenopidae	0	3	0	0	3
Sparassidae	5	2	0	1	8
Clubionidae	19	14	2	0	35
Ctenidae	3	5	2	0	10
Agelenidae	1	0	0	1	2
Pisauridae	7	1	3	2	13
Lycosidae	7	7	0	0	14
Senoculidae	2	1	0	0	3
Oxyopidae	5	3	1	1	10
Attidae	60	55	7	8	130
Dysderidae	0	1	0	0	1
Zodariidae	1	0	0	0	1
Palpimanidae	1	0	0	0	1
Total	184	205	37	77	503
Per cent.	36.58	40.75	7.36	15.31	100

my paper in 1925. I do this here for the purpose of facilitating comparison between this table, the table published in my paper and the second table in which I give an analysis of the total number of species now known to occur in Panama.

It will be seen at once that, far from showing "affinity with South America," the spiders studied by Banks are preponderantly Central American in character, since only

10.83 per cent. are distinctly South American, while fully 40 per cent. are Central American and 29.58 per cent. are indigenous. Neotropical, cosmotropical and cosmopolitan species constituting only 19.59 per cent. are always of uncertain origin. But, if we were to divide these in half and ascribe one half to South American and the other half to Central American original stock, the result would remain the same. Nay, even if we were to add these species altogether to the South American column, we still would have 69.58 per cent. of spiders which do not occur in South America. This is an incontrovertible fact.

Before continuing our analysis of the first table, let us now examine the second. This table represents all spiders recorded up to date from Panama and includes, therefore, the species recorded by Banks. The Central American affiliation of the spider fauna of Panama is in this case, as is natural to expect, still more apparent. The fauna of any country shows an increasing admixture of species found in adjoining countries as we approach the borders. In the case of Panama, however, a comparison of the two tables shows that the *relative* number of Central American species remains practically the same for the lower regions alone as for the entire state, namely 40 per cent. This is a highly significant fact. It means that *the invasion of the lower regions of Panama from South America took place at the expense of indigenous species* to the amount of 7 per cent. Of these only 3.5 per cent. are distinctly South American, while the other 3.5 per cent. occur also in Central America and therefore may have entered Panama from Central America. At least the *direction* of the migration of these 3.5 per cent. remains for the present unknown. But the picture of what has happened in Panama in the past and is probably still going on at the present time is now becoming more or less clear. As the land emerged from the sea toward the end of the Mesozoic or the beginning of the Coenozoic and the Costa Rica-Panama bridge between South and

Central America was completed, the invasion of spiders into Panama began at both ends, but was vastly greater from Central America than from South America. Why this should be so can not be answered satisfactorily at present, but it may be suggested that higher regions presented for a long time more favorable conditions for both plant and animal life. Another reason may be sought in the prevalent direction of local air currents. This brings us to a detailed analysis which is possible only when we take under consideration the methods of dispersal and the habits of spiders.

The first fact which strikes our attention is that two families are particularly rich in neotropical, cosmotropical and cosmopolitan species. They are the Argiopidae, or Orb-weavers, and the Theridiidae. A little over 33 per cent. of the latter belong to this group, while of the former a little over 26 per cent. belong to it, if we consider the entire state, or almost 35 per cent. if we limit ourselves to the lower regions of Panama. The species belonging to these two families, at least those on record from Panama, make their webs in different surroundings, on plants, on rocks, on buildings, etc., and deposit their eggs in cocoons which they either suspend in their webs or attach to foliage, branches or other objects. The habit of each species in this, as in other respects, is usually fixed in all spiders. In general one may say, therefore, that these spiders may be dispersed in any way known for spiders, by land migration, transportation by man, floating objects, ballooning in gentle air currents and, in the case of cocoons, by gales and hurricanes. Of the genus Latrodectus, which is Panamerican and exceedingly common in certain countries, we have direct evidence that it is being spread by human agency to quite a considerable extent, though there is no record of it ballooning. Yet this common spider is absent from Banks's list and evidently does not occur in the lower regions although it has been recorded from other localities in Panama. Banks lists seven species belonging to the

group of Argyrodini. Three of these are South American, three neotropical and one Mexican. The majority of species belonging to this group follow, as a rule, the distribution of Orb-weaving spiders, mainly of the genera Argiope and Nephila, with whom they live in an association of space relationship inasmuch as they use the orb-webs as foundation for their own webs. For all we know, they may be of very recent importation and, at any rate, the peculiar habits of the group show how dangerous it could be if we were to draw any conclusions from the mere listing of such spiders.

But let us return to the analysis of the first table. Of the very large family Theraphosidae there is only one species in the lower regions of Panama and that species is indigenous. There are many species of this family in Central America and still more in South America. Apparently none of the Theraphosidae balloon, but both adults and cocoons have been transported many times by man with fruit and wood to various countries. While ineffective in the case of importation of tropical species into temperate climate, this method should be effective when a tropical species is imported into another tropical country of about the same character. Yet even *Avicularia avicularia,* which is the most commonly transported species on account of its habit of making tents of heavy silk in trunks and branches of trees, in bunches of fruit, in plants, on lumber, etc., and which is quite common in Brazil, Venezuela and Trinidad, has not as yet been recorded from Panama. Three other families, namely, the Drassidae, Zodariidae and Palpimanidae, are represented by only indigenous species in Panama. Three families, the Dipluridae, Acanthoctenidae and Filistatidae, are represented by a single neotropical species each, all three with very wide distribution. The habits of the Acanthoctenidae are not known. The Filistatidae include a single genus Filistata, and this genus has six American species of which only one, *F. hibernalis,* extends from Argentina all the way to the Southern United States.

Owing to its habit of building a web on the walls of human habitations, its distribution is probably due to human agency. The case of *Ischnothele guianensis* of the family Dipluridae is less clear, but importation by man is also probable, because the species makes heavy funnel webs on plants. At any rate, none of these three families is of any use in the discussion of our problem until other species will be found. One family, the Caponiidae, is represented by a single South American species, *Nops maculata,* and deserves special attention on this account. Simon has described this species from a single, very immature ("valde immatura") specimen which he captured under a rock in Caracas, and his description occupies only six lines. Nobody has given any description of a mature specimen of either sex since Simon's publication. A confusion of species is, therefore, not only quite possible, but very likely, and the specimen referred by Banks to the Venezuelan species must be left out of consideration as a doubtful one, until mature specimens from Caracas become available for description and comparison. Eight families, the Ctenizidae, Oonopidae, Hersiliidae, Pholcidae, Selenopidae, Sparassidae, Lycosidae and Dysderidae, have no South American representatives in Panama. Most amazing is the absence of two cosmopolitan species, *Heteropoda venatoria* of the Sparassidae, and *Smeringopus elongatus* of the Pholcidae. Like *Latrodectus mactans* already referred to, these two were previously recorded from other localities in Panama, extend in their northward distribution into southern United States and southward beyond the tropical belt, and being closely associated with man and his dwellings, stables and warehouses, follow the human race all over the world, wherein they exceed considerably Latrodectus, restricted to the Americas and adjoining islands. All eight families just mentioned show some relationship with the Central American fauna and none whatsoever with the South American one. This is, perhaps, especially interesting and clear in the case of the

Lycosidae, or ground spiders living in burrows, under rocks, and as vagabonds in meadows, fields and woods. They carry their cocoons attached to their spinnerets and take care of the young until the completion of the second moult. After that, in the temperate climate of Europe and America, the young disperse by means of ballooning in gentle air currents. Whether southern species balloon, we do not know. But if they do, then the scarcity of Central American and the complete absence of South American species in Panama may be explained only on the assumption that either there are no air currents in the direction of Panama, or that there are barriers in the path of such currents, because we know over a hundred species from the North American continent and at least ninety-three from the South American one. Yet there is only one Central American Lycosa in the lower regions of Panama, and only seven have been recorded from other regions. The families Uloboridae, Linyphiidae, Mimetidae, Clubionidae and Ctenidae and thirteen other families which we have already considered have no cosmopolitan, cosmotropical or neotropical representatives in Panama. It is strange to notice the absence of the cosmopolitan *Uloborus geniculatus* and of *U. americanus* from the lower regions of Panama, since they had been recorded from other places. The latter species, common in the United States, extends south as far as Panama and the West Indies. Of the five species recorded by Banks only one is South American, the other four being Central American. Of the four species of Linyphiidae only two are South American, although no less than five genera, including Linyphia, are known to have ballooning habits, and no less than six species of that genus are found in Costa Rica and four in Colombia. But the whole family is more characteristic of temperate climate and has more numerous representatives in the temperate zones of North and South America. The Mimetidae are predaceous vagabonds feeding chiefly on spiders. We know little of their habits, and their dis-

tribution is quite peculiar. *Gelanor zonatus* is common in Brazil and Guiana. *Mimetus bigibbosus* has been originally described from Teapa in Tabasco, Mexico. The Clubionidae, as I delimit the family, live in little tubular webs on foliage, under rocks, under bark, etc., and attach their cocoons more or less firmly to some support. It is not known whether they balloon, but ballooning is not likely. Only one of the seventeen species recorded by Banks is South American. The Ctenidae are distinctly southern spiders, living on the ground under rocks, etc. Banks lists under the same family Acanthoctenus, which I refer to a family of their own, and Lycoctenus, which is synonymous with Anchylometes and belongs in the family Pisauridae. Of the five species which undoubtedly belong in the family Ctenidae, four are Central American. Of the fifth, *Ctenus medius,* which is South American, Banks writes that the two females from Barro Colorado "agree fairly well with specimens of *Ct. medius* from southern Brazil. But . . ."—after which follow slight discrepancies and at the end "I *expect* [the italics are mine] that *medius* is the same as *Ct. ornatus* Keys., also from South Brazil." So Banks himself is not quite sure about his definition. Yet we must realize that the family Ctenidae is represented in South America by no less than ninety-three species and in Central America by only twenty-four species. It is evident that the Ctenidae, like the Theraphosidae, Ctenizidae and other spiders living on the ground, may be dispersed only by land, and that this method, for some reason, was not very successful in Panama.

The family Argiopidae we have already mentioned. Notwithstanding its large neotropical component the majority of this family in the lower regions of Panama are Central American. Of the twenty-two species listed in the fourth column of our table, neither Argiope nor Nephila balloon, yet *Nephila clavipes* and *Argiope argentata* have a very wide neotropical distribution, and

Argiope trifasciata which is cosmopolitan and which has been recorded from other localities in Panama is absent from the lower regions. The three distinctly South American species listed by Banks are *Eperia truncata, E. trispinosa* and *E. albostriata.* All three have wide distribution in South America, but for Barro Colorado Banks records only one specimen for each of the first two, and only two specimens for the third species (one from Frijoles and one from Las Sabanas). Furthermore, Banks lays great stress on the fact that *Micrathena* (*Acrosoma*) *schreibersi,* which is quite common in South America, is also common in Barro Colorado. But this species has been recorded by Cambridge from Teapa in Tabasco, Mexico, geographically a Central American locality and an inland one at that. Besides, of the ten species of Micrathena listed by Banks, not one is an exclusively South American species, while four are Central American and six neotropical, while the genus which is strictly American contains 129 species and twenty-two of these occur in Colombia. The family Argiopidae is represented by no less than 500 species in South America, yet in the lower regions of Panama eight species are indigenous, thirty are Central American, twenty-two neotropical and only three South American.

Of the remaining families the Sicariidae are represented by one South American, one Central American and two neotropical species. The latter have a very wide distribution due, presumably, to human agency, as the habits of the species seem to preclude other means of dispersal on a wide scale. The Thomisidae or crab-spiders live chiefly on foliage and are usually ballooning in the temperate zones. Of the ten species recorded by Banks only two are South American, three are neotropical, three indigenous and two Central American. The distribution of the Pisauridae, is, at present, difficult to understand. Their habits are different from those of Lycosidae with whom they are otherwise closely related. Most Pisauridae live near water and either carry their cocoon

in the mouth or attach it in a web amidst foliage. They run on water without difficulty and dive readily. Some were observed catching fish. Under the circumstances it is very likely that they are able to cross considerable stretches of water on floating objects and that therein lies the explanation of the fact that of the seven species recorded by Banks two are South American and two neotropical with wide distribution, while three are indigenous. The peculiarity of their distribution becomes more readily understood when we compare it with the distribution of the Lycosidae, from whom they differ primarily in habits and not in important structures. The family Oxyopidae is represented by five species of which one is South American, one—*Oxyopes salticus*—has a distribution from New York and New Jersey, through the Southern United States, Mexico and West Indies to Central America, Colombia, Bolivia and Brazil. One species is Central American, and two, indigenous.

The last and one of the most interesting families is the Attidae, of which 130 species are now known to occur in Panama and sixty-one in the lower regions. They are all predaceous vagabonds living on foliage, on trunks of trees, on buildings, on the ground. At least three genera are known to balloon in the temperate zones. Nevertheless, of the sixty-one species recorded by Banks, only one species, *Psecas* (*Deza*) *sumptuosa* Perty, is from South America (Brazil), although it must be added that it has been also recorded from Trinidad. Banks is mistaken when on page 72 he states that *Pachomius dybowskii* was "previously known only from South America." Peckham, who described this species in detail in his "Attidae of Central America," says on page 82, "We have numerous specimens from Guatemala, New Grenada and French Guiana." In this case a confusion of species is out of the question. Two of the sixty-one Attidae are cosmopolitan, namely, *Menemerus bivittatus* and *Plexippus paykulli*. Both live on walls of buildings, feeding chiefly on domestic flies, and follow human trade in their

distribution. It is not uncommon to capture them on board transoceanic steamers. Two species are neotropical with fairly wide distribution. The rest are either indigenous (twenty-six) or Central American (thirty). Yet there are as many as 463 well-described, strictly South American species, not one of which has been recorded from any locality in Panama. Nor does this figure include species once described under the now obsolete genus Attus, to the number of seventy-six from South America alone. There is evidently some barrier to the effective migration of South American Attidae northward, while no such barrier obstructs the southward migration of Central American Attidae into Panama.

The conclusion to be drawn from this detailed analysis of spiders collected in the lower regions of Panama can be only one and is entirely beyond any dispute: The spider fauna of Panama is Central American in character, and the transition from Panama to South America is fairly abrupt. Far from upsetting the evidence on which I based this statement in 1925, Banks has unwittingly contributed very important additional evidence in its support and nothing whatsoever to its refutation.

SHORTER ARTICLES AND DISCUSSION

HYBRID SUNFLOWERS

THE appearance of Dr. E. E. Watson's "Contributions to a Monograph of the Genus Helianthus"[1] will undoubtedly stimulate new interest in the sunflowers all over the country. The treatment is comparatively brief, and not monographic, but very thorough so far as it goes, and represents a vast amount of careful work. The number of species given, for North and South America combined, is 108. Three forms described as species have been entirely overlooked. These are *H. coloradensis* (common in Colorado; cultivated at Kew), *H. alexandri* (Michigan) and *H. nebrascensis* (Nebraska). Although I marvel at the skill and industry of the author, compared with which my own labors in the same field are of small account, I venture to think that his outlook is, in some respects, rather narrow and conventional. As he himself says, on page 435, in criticizing another man, "Psychology plays havoc with systematic botany." Thus he says that certain plants are "of interest to students of genetics, but only incidental to our systematic study"; but what is a systematic study, in the long run, but a study of genetics? Genetics constitutes the dynamic aspect of taxonomy. What he really means, in this and other passages, is that he is concerned with species, and any process that does not result in species is, for the purpose in hand, of no particular consequence. Yet it must be that through the processes of variation or mutation species eventually arise, and it is legitimate to argue that a taxonomist should not merely ask what species exist, but also how came they to exist? Through the answers to the latter question, so far as they can be obtained, a natural classification may be built up. It results from such a point of view that no fact of morphology or variation is wholly insignificant and even chemical reactions have to be taken into account, although descriptions of them scandalized another student of Compositae several years ago. It strikes me as an especially weak point in the paper that no serious attention is given to hybridization.[2] Dr. Watson even makes the extra-

[1] Papers Michigan Acad. Science, Arts and Letters, IX, 1929.

[2] Yet he makes this significant statement, although it can not be of universal application in the genus: "Intergrading forms are to be found

ordinary statement (p. 338) that there is no evidence for Gray's statement that *H. argophyllus* hybridizes freely with *H. annuus*. I have proved experimentally that it hybridizes with the greatest ease, and will do so whenever the pollen of one is conveyed (as by bees) to the other. Indeed, this hybrid was recorded by W. Robinson in "English Flower Garden," 1905, who mentions the horticultural name *H. dammanni* as supposedly applicable to it. In 1916, Sazyperow[3] describes the same hybrid, which was made with the object of getting a plant resistant to rust and other diseases. I gave a good figure of the hybrid in *American Museum Journal*, 1918, p. 41.

In former years several hybrids of *Helianthus* were obtained in my wife's cultures in Boulder. The hybrids *H. orgyalis* × *maximiliani*,[4] and *H. annuus* × *petiolaris*[5] were fully described. Others were briefly referred to in the Standard Cyclopedia of Horticulture. As there is now little probability that I can resume this investigation, it seems well to put additional facts on record, although they are not all as decisive or clearly interpreted as could be wished.

Helianthus argophyllus × *annuus*

H. annuus pollen was used on *H. argophyllus*, the *annuus* being the var. *coronatus*, with red on the rays. The *argophyllus* flowered so late that it had to be transferred to the greenhouse, to bloom in the fall. Two plants which resulted had the manner of growth and foliage as in typical *argophyllus*, one being over seven feet high. The rays were orange, but my wife reported one which showed red on the rays (the *coronatus* used was evidently heterozygous). Of the two plants studied by me, one was normal as to rays, the other had very numerous and narrow rays, some of them short. I found in one plant that about half the pollen grains were apparently normal, in another hardly 10 per cent. appeared normal. The normal grains had a diameter (not counting spikes) of 35 to 37 μ (one was 45 μ).

My wife crossed the above *argophyllus* × *annuus* hybrid with *H. annuus* var. *vinosus* in 1915. She picked out the young plants

in large numbers which can be arranged in a regular and gradual progression, from any one of the related species to any other one, and this progression can be arranged according to any one of the various diagnostic characters, and the varying characters are not correlated."

[3] *Bull. Applied Botany*, Petrograd.

[4] *Bot. Gazette*, 67: 264, 1919.

[5] *Torreya*, 18: 11, 1918.

(probably less than half) which had *argophyllus* foliage. We got ten good plants, showing orange with chestnut on rays in three, vinous in seven. In every case the red color was in a zone round the base of the rays, sometimes invading nearly half the ray. In one vinous specimen (rays in two rows) the pale yellow part of rays has the veins delicately lined with vinous, and on the under-side the whole surface is pale with vinous lines on the veins, without any solid vinous base. These facts are of interest because we found that different species have characteristic color patterns, when the red is introduced from red *H. annuus*. The original *argophyllus* had two rows of rays, and the derivatives had two rows, but much larger heads. The plants grew more slowly than *H. annuus*, and seemed sensitive to heat.

Helianthus cucumerifolius × *annuus*

Figured in *American Museum Journal*, 18: 41, 1918; this hybrid was earlier produced in the botanic garden at Hanover by Andrée (1913), and in Sweden by Lundström (1914). *H. annuus vinosus* × pale *cucumerifolius* was named var. *evanescens* in *Journ. of Heredity*, 1915, p. 545.

H. annuus primulinus (light yellow rays) was crossed with *H. cucumerifolius purpureus* (purplish rays). The hybrid was about five feet tall, much branched, with rather shiny *cucumerifolius*-like leaves; disk very black, its diameter 33 to 36 mm; rays about 34 mm long and 12.5 wide, basal 8 mm clear lemon, rather strongly limited, the rest paler, the apical part weakly flushed with red. This red is wholly from the *cucumerifolius* side.

A different *cucumerifolius* hybrid had rays streaked along veins with red; a pretty effect, the red a rosy tint. This is an F_2 from cross with some *annuus* type, exact history not known.

A cross of *H. annuus coronātus* × *cucumerifolius purpureus* (thus getting red from both sides) gave it the F_2 segregates of two types, viz.: (1) Four feet high, spreading, much branched; stems speckled with purple; leaves dark green, very shiny, blades broad and short, strongly dentate; involucral bracts with long tapering ends (but not so long as in true *cucumerifolius*); disk small, about 25 mm diameter; rays ample, broad, numerous, with basal half rich chestnut, apical half light lemon on under-side the middle third of ray is mainly chestnut, and lateral thirds are more or less streaked on veins. Tip to tip of rays about 100 mm; disk very dark. (2) Quite like the *cucumerifolius purpureus*,

small and showing the pink tints. One plant is intermediate in size, with shiny, deeply dentate leaves; heads 114 mm across from tip to tip of rays, disk 34 mm, rays bright lemon yellow, very faintly washed or speckled with red on basal half, and sometimes more distinctly red below. One head of this plant just coming out showed the red more distinctly, dilute chestnut, covering less than basal half of ray. The involucral bracts of this plant are long, *cucumerifolius*-like, the extreme filiform tips dark.

Hybrids between Annuals and Perennials

This is the most perplexing part of the subject, greatly needing further elucidation.

Helianthus annuus × *rigidus* (hybrid *suttoni* n. hybr.)

This hybrid was reported by Thellung. My wife raised a hybrid *H. annuus coronatus* (very dark) × *rigidus* "Miss Mellish."[6] The *annuus* was the seed parent. It came into flower on September 1, 1919; a row of plants, all alike. Growth like *rigidus,* and purple stems as in *rigidus;* involucre as in *rigidus,* but twice the size; disk dark as in *rigidus,* but in that species the stigmatic branches are entirely orange, in the hybrid they have a broad light red stripe down the middle; achenes hairy as in *rigidus;* rays 24, orange, same color as *rigidus,* with no trace of red, except in one plant in which there was red on middle third of under-side of rays; rays broader than in *rigidus,* flatter, more like *annuus* in this, strongly overlapping; diameter of head about a third more than *rigidus;* upper leaves in general similar to *rigidus,* but with broader base, more shining above, and not so thick and stiff; lower leaves immense, with broad base, like *annuus.*

Previous to this, Mr. Leonard Sutton had raised *H. annuus coronatus* × *rigidus* at Reading, England, and sent me a good series of specimens. In his letter of October 21, 1914, he says:

> We thought the small-centered *H. rigidus* with its long rays would be particularly attractive if the red coloring could be worked into it, but we hardly expected the cross would produce fertile seed. The Red Sunflower was the seed parent, and we have in F_1 quite a number of types, varying from *H. rigidus* apparently pure, to others with coarser leaves, while some are exactly like the seed parents, probably the result of a few stray grains

[6] The Elliott Catalogue says: "Miss Mellish" is a variety of *H. lactiflorus,* but ours had a dark disk.

of Red Sunflower pollen. A very surprising feature is that the red coloring does not appear at all [on the rays], whereas it is of course dominant in the annual sunflowers.

On December 29, 1915, Mr. Sutton wrote: "One of our F_2 from Red Sunflower × *Harpalium rigidum* has again come like the latter (pollen) parent, but with the addition of small streaks and splashes of 'red' color in the flowers." Some F_2 seed from Sutton gave only the *H. annuus* type.

Helianthus decapetalus × *petiolaris*

Exhibited by Mr. Cowell at meeting of Torrey Botanical Club, as reported in *Bull. Torrey Bot. Club,* 23: 357, 1896. Unknown to me.

Helianthus annuus coronatus × *decapetalus multiflorus grandiflorus* hort. (single)

This cross was made by my wife, and grown in Knudsen's greenhouse, Boulder. Notes made on April 15, 1917. Small plants (because grown in greenhouse), only one in flower. Habit entirely that of the annual (which was the seed parent), but leaves narrower than usual, varying in dentition of margins. The plant in flower has bracts exactly as in *annuus;* rays bright orange, but "collarette," some partly tubular, the collarette lobes tipped with red. One plant has three leaves at each node; one has the leaves more shiny than the others. The lot is very variable, and may be keyed thus:

Stems dark purple . . . form a.
Stems green.
  Leaves three at each node . . . form b.
  Leaves two at each node, and more shiny . . . form c.
  Leaves irregular (not opposite), dull . . . form d.

Helianthus tuberosus × *annuus coronatus*

A row of plants, July, 1916, from *tuberosus* pollen on *coronatus.* All normal *coronatus,* with no sign of *tuberosus* characters. Unless there was some contamination with *annuus* pollen, these may be "false hybrids," due to stimulation without union of the gametes. Such possibilities must be taken into account in hybridizing widely different forms.

Helianthus annuus coronatus × *subrhomboideus*

Through a misunderstanding, this cross, made by my wife, was first reported as *annuus* × *pumilus.* The *annuus* was the

seed plant. The plants stayed in the rosette state a year (could not be forced in the greenhouse). They flowered near the middle of July, *H. subrhomboideus* at Boulder appearing about a couple of weeks later. The hybrid was very like *H. subrhomboideus,* but a much taller, stouter plant, with larger leaves, which are, however, serrate in the same manner; stem has the same pinkish-purple color; involucral bracts same, with same more or less pinkish tips, but bracts of hybrid more distinctly acuminate. I thought I could make out differences in the flowers, thus: (1) *subrhomboideus;* ray florets regularly with elongated but non-functional pistils, which turn brown and shrivel at end, and achenes of rays wholly glabrous, trigonal, with three large pappus scales. Disk achenes of same head hairy, both on sides and edges, and there is a complete pappus crown, connecting the scales, the whole deciduous. (2) Hybrid: ray florets wholly without pistils, and their achenes more or less hairy. Inner pappus scale of ray floret often purplish, and scales of disk florets often stained in the same way. Disk florets with only two scales, no crown.

However, I later found a wild *H. subrhomboideus* wholly lacking pistils in ray florets, and a hybrid was found with supernumerary scales between the two long ones on the achenes. The rays of the hybrid were entirely orange; disk dark, the lobes of disk corollas deep red, and ends of disk bracts dark. The root system was that of *H. subrhomboideus,* with "earth branches."

H. subrhomboideus Rydb. is treated by Watson as a synonym of *H. rigidus.* It is the dry-country representative of that species, and seemed to me sufficiently distinct. It remains to be seen, however, what it would do if transplanted to a moister region. The type was from Whitman, Nebraska. J. M. Bates, of Red Cloud, Nebraska, wrote me that he thought the species very doubtful.

While on sunflowers I take occasion to record *Helianthus annuus* mut. *inornatus,* nov., wholly without rays, which appeared in our cultures in Boulder. The disk is dark, 45 mm diameter. Various species of Compositae are characterized by the absence of rays.

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THE VIABILITY OF CERTAIN INFUSORIAN CYSTS[1]

RECORDS of the viability of protozoan cysts chiefly refer to organisms belonging to the Sarcodina and Mastigophora. Although Goodey (15) has shown that soil amebae and flagellates may live in a resting condition for forty-nine years, there are no such records for the continued life of infusorian cysts. Maupas (88) recovered *Gastrostyla steinii* Englemann from cysts which had been dry for twenty-two months. Nussbaum (89) showed that *Gastrostyla vorax* could be recovered from cysts that had been dry for somewhat over three years, but that these cysts were not viable after being kept dry for twelve years. Fauré-Fremiet (10) in reporting some unpublished data of Balbiani stated that *Mycterothrix tuamotuensis* was recovered from cysts after remaining dry for nearly four and one quarter years. Incidentally, *Colpoda* was recovered from cysts during the same time. Neither *Colpoda* nor *Mycterothrix* was recovered from cysts after fourteen years in the dry condition. Mast (17) has reported that cysts of *Didinium nasutum* kept sealed in an air-tight vial were found to be viable after nearly five years.

On May 1, 1925, a quantity of dried standing stalks of grass was collected from a pasture adjoining Harvard House in Soledad, Cuba. This grass has been kept in a cardboard box in a drawer of a room in the Zoological Laboratory at Harvard University during the entire period since it was brought from Cuba. This box has been opened only for the purpose of taking out the small quantities of grass necessary for the different infusions that have been made in sterile water on several occasions since it was collected.

Infusion A. This was made up by placing a quantity of the grass in a finger-bowl and covering with Pureoxia distilled water. Unfortunately, accurate records of this culture were not kept. It was made up during the first week in October, 1925, and during the succeeding month the most noticeable organism was *Colpoda cucullus* Ehrbg. There was observed also a small suctorian agreeing in many essential respects with the description of *Podophrya fixa* Ehrbg.

Infusion B. This infusion was made up on January 7, 1926, a small quantity of the grass being placed in boiled tap-water.

[1] Based in part on studies made at Harvard Botanical Garden and Biological Laboratory (Atkins Foundation), Soledad, Cienfuegos, Cuba.

On January 8 *Colpoda cucullus* and several nematodes were observed. The colpodas increased rapidly in numbers until January 13. Several unidentified species of small flagellate were observed on January 12. On the same day *Oxytricha* sp. (*platystoma?*) was first observed. This hypotrich increased in numbers until January 22, when observations were discontinued.

Infusion C. This was also made up on January 7, 1926, but with distilled water. The history of this culture is practically the same as that of Infusion B, except that the various species were one or two days later in making their appearance. No suctorians were observed in either of these cultures.

Infusion D. Made up January 15, 1926, with Pureoxia distilled water. In addition to *Colpoda, Oxytricha* and small flagellates, several small myxomycete plasmodia were observed in this infusion about two weeks later. These were cultured in the Harvard Botanical Laboratory by Mr. F. A. Gilbert, who was successful in obtaining the fruiting bodies and identified the organism as *Physarum cinereum* Pers.

Infusion E. Made up February 11, 1926, with Pureoxia distilled water. *C. cucullus* appeared February 12. On February 13 the colpodas had multiplied to a considerable extent and showed noticable diversity in size. Numbers of small flagellates were also seen. On February 15, besides *Colpoda* and the flagellates, *Spathidium spathula* O. F. M. and *Oxytricha* of the same species reported for Infusion B were observed. On February 19 the suctorian (*Podophrya fixa*) was again observed.

Infusion F. This infusion was made up on May 8, 1929, in a sterile finger-bowl with sterile pond water. On the following day a few large *Colpoda cucullus* were observed. On May 10 these were considerably more numerous and showed noticeable variation in size. The smaller colpodas agreed very well in size and other details of structure with *Colpoda steinii* Maupas, but upon isolating a few of these and placing them in sterile medium it was found that they gave rise to larger forms typical of the species *Colpoda cucullus* Ehrbg. On May 12 the hypotrich, *Oxytricha* sp., presumably the same as had previously appeared in Infusion B, January 12, 1926, etc., and *Spathidium spathula* were again observed. These latter organisms did not increase in numbers to any appreciable extent.

Infusion G. This infusion was made up in the same manner as Infusion F on May 20, 1929, at 10:30 A. M. By 4:30 P. M.

on the following day considerable numbers of small colpodas, few of the larger ones and two spathidia were seen. No hypotrichs were observed in this culture.

From a subculture of this infusion made in a Syracuse watch-glass with a few small pieces of the original grass from Infusion G in sterile hay infusion medium small myxomycete plasmodia were again seen, which are believed to be the same species, *Physarum cinereum* Pers., originally observed in Infusion D in January, 1926.

A small number of nematodes was observed in this infusion on May 29. These have been identified by Dr. N. A. Cobb, of the U. S. Department of Agriculture, Washington, as species of *Cephalobus,* probably *C. elongatus.*

It is the intention of the authors to make infusions from the remaining stock of this grass at regular intervals during the next few years and it is hoped that an accurate record of the viability of the cysts of the various Infusoria which have appeared in these cultures will be obtained. It is clear from these records that cysts of *Oxytricha* sp., *Spathidium spathula* and *Colpoda cucullus* can remain viable in the dry condition for at least four years, and that cysts of *Podophrya fixa* may live in the same condition for at least nine months.

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THE DOMINANCE OF BAR OVER INFRA-BAR IN DROSOPHILA

THE intensive study of the bar gene of *Drosophila melanogaster* by Zeleny and his students and by Sturtevant has revealed many remarkable features. Attention does not seem to have been called, however, to certain dominance relations which may be of significance.

The series consists of three more or less ordinary allelomorphs: that of wild type (round eye); bar eye, which traces to a single mutation from round, and infra-bar which traces to a single mutation from bar. In addition are three double genes: ultra or double bar, bar-infra-bar and double infra-bar, which are produced with measurable frequency by homozygous bar, bar heterozygous for infra-bar, and homozygous infra-bar, respectively, accompanied by the appearance of mutant round eye. Sturtevant and Morgan have shown that the mutation process in these cases is, at least as a rule, one of unequal crossing over at the locus, such that both allelomorphs get into the same chromosome, leaving no allelomorph in the other chromosome. The fact that no difference has been detected between the round eye, which arises by demonstrable loss of the bar gene, and ordinary round eye has suggested that the relation of bar to round is a real example of presence and absence, which probably implies that the original mutation from round to bar was a translocation. Such an origin might also be related to the so far unique behavior in crossing over.

Bar and infra-bar and their double types are all well known to show imperfect dominance over round eye. The fact that infra-bar is virtually indistinguishable in its effects from bar in all combinations, as long as there is at least one true bar gene present, *i.e.*, is almost or quite completely recessive to bar, does not seem to have been pointed out. The mode of inactivation in infra-bar, however, can not be compared to a loss in quantity of the bar gene, as Goldschmidt has suggested. A similar conclusion has, of course, been indicated by Luce's discovery of a temperature reaction in infra-bar, opposite in sign to that of bar. These relations might be represented symbolically by writing the bar gene as BI, infra-bar as Bi and the corresponding locus in round eye as O, without implying that B and I are necessarily more than two properties of a single gene. The table below,

using the more convenient symbols B, B′ and O, is a rearrangement of the averages published by Morgan, Sturtevant and Bridges in *Bibliographia Genetica* (1925). The position effect noted by Sturtevant in the relation of bar and infra-bar to round eye does not seem to hold in their relation to each other, making it unnecessary, for example, to put $\frac{BB}{B'B'}$ and $\frac{BB'}{BB'}$ in different categories, as is done for $\frac{BB}{O}$ and $\frac{B}{B}$.

	4 B or B′	3 B or B′	2 B or B′ together	2 B or B′ apart	1 B or B′	No B or B′
Females At least one B	$\frac{BB}{BB}$ 25.0	$\frac{BB}{B}$ 36.4	$\frac{BB}{O}$ 45.4	$\frac{B}{B}$ 68.1	$\frac{B}{O}$ 358.4	
	$\frac{BB}{BB'}$ 24.1	$\frac{BB}{B'}$ 41.8	$\frac{BB'}{O}$ 50.5	$\frac{B}{B'}$ 73.5		
	$\frac{BB}{B'B'}$ 26.7	$\frac{BB'}{B}$ 37.0				
	$\frac{BB'}{BB'}$ 26.7	$\frac{BB'}{B'}$ 37.8				
	$\frac{BB'}{B'B'}$ 27.9	$\frac{B'B'}{B}$ 38.3				
Average	26.1	38.3	48.0	70.8	358.4	
No B.....	$\frac{B'B'}{B'B'}$ 38.2	$\frac{B'B'}{B'}$ 138	$\frac{B'B'}{O}$ 200.2	$\frac{B'}{B'}$ 320.4	$\frac{B'}{O}$ 716.4	$\frac{O}{O}$ 779.4
Males At least one B			$\frac{BB}{>}$ 29.0		$\frac{B}{>}$ 84.4	
			$\frac{BB'}{>}$ 29.7			
Average			29.4		84.4	
No B.....			$\frac{B'B'}{>}$ 46.0		$\frac{B'}{>}$ 478.1	$\frac{O}{>}$ 738.8

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